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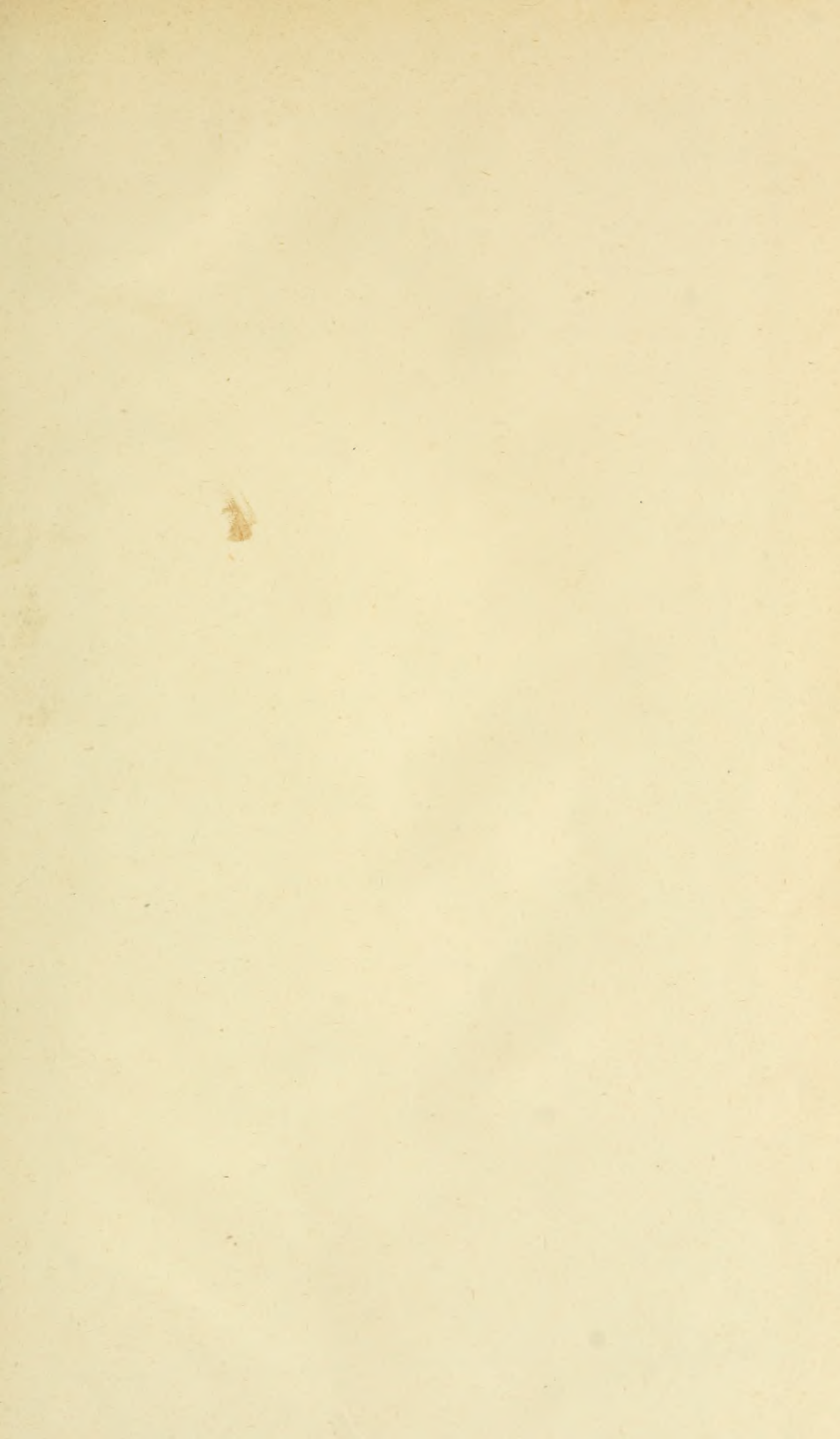
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EDITED BY

E. RAY LANKESTER, M.A., LL.D., F.R.S.,  
*Fellow of Exeter College, Oxford, and Jodrell Professor of Zoology in University College,  
London;*

WITH THE CO-OPERATION OF

W. T. THISELTON DYER, M.A., C.M.G., F.R.S.,  
*Assistant Director of the Royal Gardens, Kew,*

E. KLEIN, M.D., F.R.S.,  
*Joint-Lecturer on General Anatomy and Physiology in the Medical School of St. Bartholomew's Hospital,  
London.*

H. N. MOSELEY, M.A., LL.D., F.R.S.,  
*Linacre Professor of Human and Comparative Anatomy in the University of Oxford,*

AND

ADAM SEDGWICK, M.A.,  
*Fellow and Assistant-Lecturer of Trinity College, Cambridge.*

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**CONTENTS OF SUPPLEMENT, 1885.—New Series.**

**MEMOIRS:**

	PAGE
The Circulatory and Nephridial Apparatus of the Nemertea. By A. C. OUDEMANS, Conservator at the Zoological Museum of the University of Utrecht. (With Plates I, II, and III) . . . . .	1
The Later Stages in the Development of <i>Balanoglossus Kowalevskii</i> , with a Suggestion as to the Affinities of the Enteropneusta. By W. BATESON, B.A., Scholar of St. John's College, Cambridge. (With Plates IV, V, VI, VII, VIII, and IX) . . . . .	81
Some Notes on the Early Development of the <i>Rana temporaria</i> . By W. BALDWIN SPENCER, B.A., Scholar of Exeter College, Oxford. (With Plate X) . . . . .	123
Notes on Echinoderm Morphology, No. IX. On the Vascular System of the Urchins. By P. HERBERT CARPENTER, D.Sc., Assistant Master at Eton College . . . . .	139

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# The Circulatory and Nephridial Apparatus of the Nemertea.

By

**A. C. Oudemans,**

Conservator at the Zoological Museum of the University of Utrecht.

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With Plates I, II and III.

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THIS paper was originally written in the Dutch language and served as a "specimen inaugurale" for obtaining the Doctorate in the Faculty of Natural Science at the University of Utrecht.

The subject has been subdivided by me under the following heads :

- a.* History of the subject.
- b.* Enumeration of the investigated species and description of the method applied.
- c.* Description of the new genus *Carinoma* (= *Valencinia* Armandi, McInt.), and comparison of *Carinoma* with *Carinella*, *Cephalotrix* and *Valencinia*.
- d.* Results of the investigation.
- e.* Summary.
- f.* Literature of the subject.
- g.* Explanation of the plates.

## *a.* HISTORY OF THE SUBJECT.

It was DELLE CHIAJE (1, 2) who first discovered the blood-vessels or circulatory apparatus of the Nemertea. In the

description of his *Polia siphunculus* (= *Cerebratulus marginatus*, Ren.) he describes it as follows :

"Dalla fine della bocca principia una piccolissima vena, che sull' intestino manda un vasellino ad ogni sua borsa laterale" (l. p. 434).

His figure (Tav. xxviii, fig. 3) very clearly shows both the dorsal vessel and the smaller transverse vessels situated one above each diverticulum of the intestine.

DUGÈS (3) is the next to mention blood-vessels in the different species of his genus *Prostoma* (= *Tetrastemma*). He mentions one median and four (!) lateral longitudinal vessels, two on each side, communicating with each other in the head.

JOHNSTON (4) erroneously regarded the brain as a double heart, the longitudinal nerve-stems as vessels. Several later authors have fallen into the same error.

RATHKE (5) carefully avoided it and describes the median and the two lateral longitudinal vessels of Lineus.

QUATREFAGES (7) in his splendid treatise on this group of worms has given an accurate description of the circulatory system of certain *Hoploneuræ*. He, however, too peremptorily looked upon this description as applying to all *Nemertea*, whereas most considerable differences obtain in the other groups. However, his figures have found their way into most of the text-books of zoology as correctly illustrating the vascular system of the *Nemertea* indiscriminately.

His colleague BLANCHARD (6, 8, 9, 10) minutely describes injections made by him of the *Nemertean* vascular system as well as their results. It is hardly probable that he indeed succeeded in injecting the true blood-vessels; on the contrary, it may be fairly inferred that it was the proboscidian sheath which he operated upon.

The results with respect to the *Nemertean* vascular system to which MAX SCHULTZE (11, 12), KEFERSTEIN (14), VAN BENEDEN (13), and CLAPARÈDE (15) have been led by their respective researches, have been carefully recorded

by McINTOSH in his splendid Monograph on the group (18); I can here be satisfied with referring to that standard work.

McINTOSH himself made a very marked advance in our knowledge of the subject here treated, by detecting and clearly describing the difference between the vascular apparatus of the Hoplo- and of the Schizonemertea, more especially with respect to an interesting particularity obtaining in the œso-phageal region of the latter group where a system of spacious lacunæ surrounds this portion of the intestine, merging into the three typical vessels at a point further back towards the tail. He, however, erroneously looks upon these lacunæ as the direct continuation of the median blood-vessels. He ascribes a respiratory meaning to this lacunar arrangement.

McINTOSH similarly discriminated the differences occurring in certain Palæonemertea, where he mentions the two spacious lateral vessels of Cephalotrix and Carinella being the only portions that constitute the circulatory apparatus.

RAY LANKESTER (17) and HUBRECHT (19, 20, 21) have called attention to the presence of hæmoglobin in the circulatory fluid of Nemertea. It is, however, not improbable that the former operated not upon *Polia sanguirubra*, Quatr., as he indicates, but upon *Cerebratulus urticans* (J. Müll.), Hubr. In the latter species it is, however, not the blood but the proboscidian fluid that contains hæmoglobin, as demonstrated by HUBRECHT. The latter found it impregnating the blood-corpuscles of *Drepanophorus*.

In 1875 McINTOSH (24) describes a communication which he says exists between the proboscidian chamber and the cavity of the vascular apparatus. This observation has hitherto remained unconfirmed, although I have myself tried to test it in all the different species I investigated.

This author's description of the circulatory channels of *Valencinia Armandi* (= *Carinoma mihi*) (25) is noticed further on. In 1876 he figures the curious passage (26) of



the median dorsal vessel into the proboscidian chamber (the cavities, however, remaining separate) in the œsophageal region, without, however, following up the further course of this vessel anteriorly.

The description which BARROIS (29) gives of the blood-vessels of the Nemertea is eminently fantastic and in no respect borne out by direct observation of sections. He denies the presence of transverse vessels in the unarmed species (although DELLE CHIAJE, BLANCHARD, KEFERSTEIN, McINTOSH, and HUBRECHT vouch for them!), and looks upon the genital sacs as establishing a direct and metamerically arranged communication between the longitudinal vessels; these sacs thus forming part of the circulatory apparatus! He, moreover, mentions a posterior communication between the proboscidian sheath and the median blood-vessel. I would venture to suggest that it is the more or less complicated lacunar arrangement in the œsophageal region that has led astray in this respect so conscientious and accurate a naturalist.

The circulatory apparatus of *Malacobdella* has been investigated by BLANCHARD (6), SEMPER (28), HOFFMANN (30), and VON KENNEL (31). The latter furnishing by far the most accurate description.

GRAFF (37), GULLIVER (36), and DEWOLETZKY (38), have not materially added to our knowledge of the circulatory apparatus.

With respect to the nephridia this historical introduction can be very concise. It is the merit of VON KENNEL (31) to have correctly traced this system in different species, and to have given most satisfactory histological descriptions of it.

There is reason to suppose, however, that already DELLE CHIAJE (1, 2) was aware of its existence, and actually observed it in one of his species (*Descrizione*, p. 128, vol. iii). It has since been noticed by MAX SCHULTZE (11, 12), and more reservedly been referred to by HUBRECHT (19).

McINTOSH (18) denies its existence, and suggests that MAX SCHULTZE has confounded the circulatory with the excretory apparatus.



SEMPER (28) was the first to notice the nephridia of *Malacobdella*.

b. ENUMERATION OF THE SPECIES INVESTIGATED AND DESCRIPTION OF THE METHOD APPLIED.

The Nemerteans are divided by HUBRECHT (35) into *Palæonemertea*, *Schizonemertea*, and *Hoplonemertea*. I will adhere to this division, as it seems to me to be more natural than that of MAX SCHULTZE (11, 12), who divide the Nemerteans into *Enopla* and *Anopla*, the proboscis being armed with a central stylet or not. In regard to the fourth group, that of the *Malacobdellidæ*, formed by VON KENNEL (31), I can hardly agree with the creation of this new subdivision, the anatomical characters of *Malacobdella* showing it to be a *Hoplonemertean*, which, probably by its parasitical habit, has lost stylet and eyes, and has obtained in the hindmost part of its back an attaching apparatus wherewith to fix itself to its hosts (*Mya*, *Pholas*, &c.). The absence of cephalic sacs cannot be a reason for removing it from the *Hoplonemertea*, as *Amphiporus hastatus*, McInt., a true *Hoplonemertean*, is also deprived of these organs.

Of each of these three groups I have examined examples. All the specimens I have used are from the collection of Prof. Hubrecht, who with the greatest kindness not only put the specimens in spirit at my disposal, but allowed me to examine his numerous collection of microscopical slides and series of sections. I was thus enabled to examine specimens of all the ten families: *Cephalotricidæ*, *Carinellidæ*, *Poliidæ*, *Valenciinidæ*, *Lineidæ*, *Langiidæ*, *Amphiporidæ*, *Tetrastemmidæ*, *Nemertidæ*, and *Malacobdellidæ*. Only of the genera *Borlasia*, Oken (emend. McInt.) (*Lineidæ*), *Prosorhochmus*, Kef. (*Tetrastemmidæ*), and *Oerstedtia*, Quatr. (*Nemertidæ*), I have not examined representatives.

The new automatic microtome of Caldwell from Cambridge has very much facilitated my research. As the Nemerteans are animals which cannot be submitted to the usual methods of

dissection, but can only be satisfactorily studied when cut into microscopical slices, it is easily understood that such research can only be made by examining a complete series of slices of the same animal. This may be performed very easily when using the microtome of Caldwell, and the sticking-method of Giesbrecht.

The thickness of the slices varied between  $\frac{1}{70}$  and  $\frac{1}{100}$  millim. So I obtained series of

*Cephalotrix linearis* (Rathke), Oerst., one specimen, transversally, the foremost part to the intestine (230 slices).

*Carinella annulata* (Mont.), McInt., three specimens transversally, of each, the foremost part to the intestine (behind the nephridial system), (resp. 730, 800, or 2550 slices).

*Valencinia Armandi*, McInt., one specimen, transversally, the foremost part to the intestine (behind the nephridial system) (880 slices), and the tail.

*Valencinia longirostris*, Quatr., one specimen, transversally, totally (2300 slices) cut up.

One specimen, partly sagittally partly transversally (1940 slices).

One specimen, the head transversally (200 slices), a piece of the intestinal region sagittally (138 slices), and the tail transversally (130 slices).

*Polia curta*, Hubr., one specimen, *in toto*, transversally (1150 slices).

*Lineus sanguineus* (Rathke), McInt., one specimen, with a large piece of the intestinal region, transversally (735 slices).

One specimen, young, *in toto* (720 slices), transversally.

One specimen, young, the head, transversally (150 slices), the œsophageal and a piece of the intestinal region sagittally (120 slices) and the tail transversally (200 slices).

One specimen, intestinal region, sagittally (140 slices).

*Lineus gesserensis* (O.F.M.) McInt., one specimen, the foremost part with a large portion of the intestinal region, transversally (1125 slices).

*Amphiporus lactifloreus* (Johnst.), McInt., one specimen, *in toto* (840 slices), transversally.

*Amphiporus pulcher* (Johnst.) McInt., one specimen, *in toto*, transversally (700 slices).

*Amphiporus hastatus*, McInt., one specimen, transversally (1200 slices).

*Drepanophorus rubrostriatus*, Hubr., two specimens, transversally, *in toto* (resp. 800 and 1300 slices).

*Tetrastemma candidum* (O.F.M.), Oerst., one specimen, transversally, *in toto* (580 slices).

*Malacobdella grossa* (O.F.M.), Blainv., two specimens, transversally (resp. 423 and 428 slices), and one specimen, the foremost half horizontally (130 slices).

Total, 20,639 sections.

Moreover, from the collection of Prof. Hubrecht I made use of preparations of *Cephalotrix linearis* (Rathke), Oerst., *Carinella annulata* (Mont.), McInt., *Valencinia longirostris*, Quatr., *Polia curta*, Hubr., *Cerebratulus marginatus*, Ren., *Cerebratulus hepaticus*, Hubr., *Cerebratulus urticans* (J. Müll.), Hubr., *Cerebratulus roseus* (d. Chiaje), Hubr., *Langia formosa*, Hubr., *Amphiporus pulcher* (Johnst.), McInt., *Amphiporus marmoratus*, Hubr., *Amphiporus hastatus*, McInt., *Drepanophorus rubrostriatus*, Hubr., and *Nemertes gracilis*, Johnst.

c. DESCRIPTION OF THE NEW GENUS CARINOMA (= VALENCINIA ARMANDI, MCINT.), AND COMPARISON OF CARINOMA WITH CARINELLA, CEPHALOTRIX, AND VALENCINIA.

Amongst the above-mentioned Nemerteans there also occurs the name of *Valencinia Armandi*, McInt. Of this species I was able to examine a specimen which was caught and named by McIntosh himself (one of the type specimens) and presented to Professor Hubrecht. Even after a superficial examination, it appeared necessary to remove it from the genus *Valencinia*, Quatr. By the situation of the

mouth behind the ganglia, and by the absence of one or more stylets in the proboscis, and of deep lateral furrows on the head, this species, it is true, is a Palæonemertean; but by the absence of diverticula of the intestine, of posterior lobes, and of cephalic sacs, it approaches more closely to the group wherein Hubrecht has placed the families of the Carinellidæ and Cephalotricidæ. I am compelled to make a new genus for this species, to which genus I will give the name of *Carinoma*. The species thus is called *Carinoma Armandi* (McInt.), Oud. In the following pages this proceeding will find its justification.

The chief reason McIntosh (25) had for placing this species in the genus *Valencinia* was a certain agreement between this species and the one formerly described by him as *Valencinia lineformis* (18). McIntosh, however, made a mistake in, arranging a new worm in a genus (*Valencinia*, Quatr.) which he did not know by personal investigation. Sections through a specimen of *Valencinia longirostris*—the species which had served as type to the genus *Valencinia*—would have convinced him very soon that *Valencinia Armandi* can in no case be placed in this genus, whilst *V. lineformis*, McInt., probably is a synonym of *V. longirostris*, Quatr.—at least is considered so by Hubrecht (31).<sup>1</sup>

It will suffice if I explain by what facts especially *V. Armandi* and *V. longirostris* differ from one another, facts which can at the same time serve to characterise the new genus which is created for *V. Armandi*, and to show that the relation to *Carinella* is more intimate.

McIntosh describes *V. Armandi* in detail, so that I can here be satisfied with a short recapitulation.

<sup>1</sup> In my opinion it is certain, both from the description of *V. lineformis* in his Monograph (18), as from the anatomical facts given in his treatise on *Val. Armandi* (25), that *V. lineformis* is, just as little as the other, a *Valencinia*, but a form which approaches closely to *Cephalotrix linearis* (Rathke), Oerst. *V. lineformis*, viz. has two muscular layers (one circular and one longitudinal) within its basal membrane, only two great longitudinal vascular trunks and two lacunæ in the head, and the lateral nerves are situated between the fibres of the longitudinal muscular coat.



Along the whole length of the body there are two muscular coats within the basal membrane, a circular layer and a longitudinal one. In the head and in the œsophageal region a third layer occurs between the outer (circular) layer and the basal membrane, viz. a layer of isolated bundles of longitudinal muscular fibres. The bundles are separated from one another by hyaline basal tissue. In the œsophageal region a number of fibres of the circular muscular coat of the proboscidian sheath direct themselves round the œsophagus. Further backwards they increase in number, whilst they diminish beneath the proboscidian sheath. At last there is no muscular fibre between proboscidian sheath and intestine, and a little more backwards the process repeats itself in a reverse manner, so that the proboscidian sheath is again surrounded by its circular muscle, and no more fibres go round the intestine. Further, here and there in the head and the post cerebral region more transverse bands of fibres appear, which, however, are of secondary importance.

The brain is situated outside of the two characteristic muscular coats, though the above-mentioned layers of isolated longitudinal bundles are situated externally to the brain.

Also the two lateral nerves lie in the œsophageal region outside of the two muscular coats, penetrate a little further backwards into the circular coat, and gradually come to lie between the longitudinal muscular fibres, moving still a little further again outwards, remaining, however, between the two layers.

The intestine has no diverticula.

Of the vascular system I will treat afterwards. In truth, in regard to this system, I can correct McIntosh only in one respect, viz. in regard to the mutual communication of the six vascular trunks.

The mouth is situated behind the ganglia.

The proboscis has no stylet.

The head has no deep lateral longitudinal furrows.

Posterior lobes (brain respirators, cephalic sacs) are absent.

Now let us repeat in a few words what McIntosh says concerning his *V. lineformis*: to show (1) how little it agrees with *V. Armandi*, and (2) how at the same time it differs from the type of the genus *Valencinia*, Quatr.—*V. longirostris*, Quatr.—which I hope to describe hereafter.

Through the whole length of the body we find two muscular coats within the basal membrane, a circular layer and a longitudinal layer (also in *Cephalotrix*). Of a third layer in the head (this is absent in *Cephalotrix*) and of a fourth layer in the œsophageal region, nothing is mentioned (this I have found in *Cephalotrix*).

How the brain is situated in respect to the muscular layers is not mentioned (these lie in *Cephalotrix* within the inner (longitudinal) muscular layer, just as in the *Hoplonemertean*s), but the lateral nerves through the whole length of the body lie between the longitudinal muscular fibres (just as in *Cephalotrix*).

The vascular system consists of two lacunæ of the head and two longitudinal tubes. This is typical in the *Cephalotricidæ*, and one has only to consult my description of this system in *Cephalotrix linearis* (Rathke), Oerst., to obtain an idea of the vascular system of *V. lineformis*.

McIntosh has not mentioned diverticula of the intestine (*Cephalotrix* has none).

The mouth is situated behind the ganglia, the proboscis has no stylet, the head has no lateral furrows, and the cephalic sacs are absent (all characters of *Cephalotrix* as well).

Now let us consider how these points are arranged in *Carinella*.

Through the whole length of the body there are two muscular coats, a circular layer and a longitudinal layer, both within the basal membrane. A special layer between the circular layer and the basal membrane is absent. On the other hand, we find in the œsophageal region the same layer as in *V. Armandi*, and this layer also here originates from the circular layer of the proboscidian sheath. Although this layer is in the œsophageal region more visible than elsewhere, it is

continued even further backwards. But there are always some fibres between the proboscidian sheath and the intestine, even in the œsophageal region.

The ganglia and the lateral nerves are always outside of the circular coat and within the basal membrane.

The intestinal tract has no diverticula. The mouth is situated behind the ganglia. The proboscis has no stylet, the head no lateral furrows, the brain no posterior lobes.

We shall see that the vascular system occurs in two forms. The first approaches that in *Cephalotrix*, the second that of *V. Armandi*. But this will hereafter be noticed.

I will now sum up in a few words the characters of *Valencinia* (borrowed from the typical species *longirostris* of Quatrefages) to justify my first assertion that *V. Armandi* can in no case be placed in this genus.

Within the basal membrane there are, through the whole length of the body, three muscular coats, viz. an outermost layer of longitudinal fibres, then a circular layer, and finally an innermost longitudinal one. There is no trace of an innermost circular layer inclosing the proboscidian sheath and the intestine.

The whole central nervous system lies between the circular muscular coat and the outer longitudinal one.

The whole intestinal tract has, with the exception of the œsophagus, diverticula. The mouth is placed behind the ganglia. The proboscis has no stylet, the head no lateral longitudinal furrows. But posterior lobes are present, even large, and are directly continuous with the brain.

When describing the vascular system we shall see how extraordinarily that of *Valencinia* deviates from that of *Carinella*, *Cephalotrix*, and the new genus *Carinoma*. And whoever chooses to form an opinion on this point need only compare the figures 1 (*Cephalotrix*), 2 and 4 (*Carinella*), 5 (*Carinoma*), with 13—16 (*Valencinia*).

In none of the four genera can any point of special importance be derived from the proboscidian sheath and proboscis. In the one the proboscidian sheath is long, in the other (*Cari-*

nella and Carinoma) short, and the same is the case with the proboscis.

We must now enumerate those characters which Carinoma does not share with Valencinia, and which are common to one, two, or three of the other above-mentioned genera.

In all the four genera the mouth is situated behind the ganglia, there are no stylets in the proboscis, and the lateral longitudinal furrows are absent. Thus they are all Palæonemertea.

In Valencinia well-developed posterior lobes occur, coalesced with the ganglia. Also well developed intestinal diverticula, and through the whole length of the body three well developed muscular coats. These characters at once are absent in the genera Cephalotrix, Carinella, and Carinoma.

In Valencinia the œsophageal constrictor muscle is absent, but it occurs in the three other genera. In Carinella and Cephalotrix only a part of, in Carinoma all the fibres of the proboscidian sheath are used to form it. In Carinella it extends much further backwards; there is thus formed an intestinal constrictor.

The third muscular coat of Valencinia (the first from without inwards) which is situated exteriorly to the brain, occurs in Carinoma, but much less developed and only in the head and the œsophageal region. (This, and certain peculiarities of the vascular system in the head are the only characters which are common to Carinoma and Valencinia, and not common to Carinoma and the other two genera.)

The ganglia (excluding the posterior lobes) are placed in Valencinia, Carinoma, and Carinella outside of the circular muscular coat, in Cephalotrix within this and the longitudinal one. The lateral nerves always remain to the exterior of the circular muscular layer in Valencinia and Carinella. In Carinoma they penetrate, in the hindmost half of the œsophageal region, the circular layer till they lie in the midst of the longitudinal layer, a little further backwards again moving outwards, and finally remaining between the



longitudinal and circular layers. And in *Cephalotrix*, lying already within the muscular coats, they go outwards, but do not go farther than the midst of the longitudinal layer, where they remain.

Of the vascular system I will here only note one peculiarity, viz. that *Valencinia* has a median dorsal vessel, which is absent in the three other genera.

*Carinoma Armandi* (McInt.), Oud., has the following external characters: Length to 20 c.m., width that of a stout thread (contracted and in spirits 1 mm.). Body cylindrical except the flattened head and the also flattened tail, which terminates in a long point. The foremost part of the body is whitish, the hindmost pale buff and the tail translucent. Eyes are absent.

#### d. RESULTS OF THE INVESTIGATION.

##### 1. *Cephalotrix linearis* (Rathke), Oerst., figs. 1, 19—22.

The vascular system of *Cephalotrix* consists in two longitudinal trunks, which communicate in the tip of the snout and in the tail. I had no opportunity of convincing myself of the latter fact by personal examination.

Before the ganglia we find two lacunar spaces, one on each side of the proboscidian sheath (fig. 19), which communicate in the tip of the snout (fig. 1) by means of an arch above the proboscidian sheath. This arch, too, is lacunar, that is to say, irregular in shape, and when cut transversally does not show a circular or ellipsoidal form. There are, moreover, no muscular or other fibrillar walls, though the blood-fluid, as one would be inclined to think from the expression lacunar, does not wash directly the longitudinal muscular layer, nor even do the lacunæ present themselves as gaps in the gelatinous tissue that fills up the room between the proboscidian sheath and the longitudinal muscular coat. On the contrary, though the lacunæ are imbedded in the gelatinous stroma, this is—where it forms the lining of the lumen of the lacuna—changed so that it absorbs more colouring material than elsewhere farther

from the lumen. On the inner side of these cavities I have seen here and there small flattened nuclei.

Thus the lacunæ have a wall consisting of a layer of cells with flattened nuclei, and a layer of hyaline basal tissue. McIntosh (26) makes use of the terms "granular layer" and "basal layer" or "layer of basal tissue," where he describes the wall of the proboscidian sheath.

I did not observe a communication of the two lacunæ beneath the proboscidian sheath.

On following the lacunæ backwards one sees that they pass with the proboscidian sheath through the brain ring, formed by the ganglia and their two commissures, still resting on the sides of the proboscidian sheath (fig. 20). They then descend to a lower level. The mouth and the œsophagus next become visible. First the lacunæ remain where they are (fig. 21), that is to say, they do not descend any further, but lie in the horizontal plane, between the stomodæum and the proboscidian sheath. A few slices further backwards they are separated from the proboscidian sheath by the œsophagus which assumes a semilunar shape, the two horns extending between the proboscidian sheath and the blood cavities. Now, these cavities lie against the intestine above the plane of the nerve trunks, which are perfectly lateral. Behind the œsophageal region the lacunæ descend till they come to lie against the intestine, beneath the level of the lateral nerves, but still imbedded in gelatinous stroma. However, they have become somewhat changed, having obtained outside of the hyaline basal layer a layer of circular fibres. Intentionally I use here the term "fibres" because I have not been able to make out whether they are muscular or not. It appeared to me that they were still "in statu nascenti." They are still primitive, and I cannot say anything definite concerning them. They appear to be of the same nature as those which I shall describe afterwards in *Carinoma Armandi* (see fig. 74). I have not seen longitudinal fibres. Probably the fibres add to the contractility of the vessel.

I have seen nothing of the water-vascular, better called ne-

phridial system. Hubrecht mentions (35) in the living animal on the level of the mouth a lateral opening, and adds ("of the water-vascular system?"): I can only mention that the blood spaces, seen on transverse section, here send a diverticulum towards the periphery above the lateral nerves. But I have never seen an opening, nor anything that could represent a nephridial system, such as I shall describe below in *Carinella*.

## 2. *Carinella annulata* (Mont.), McInt., figs. 2, 4, 19—27.

The vascular system consists chiefly of two longitudinal vessels, which communicate in the tip of the snout and in the tail. I have not verified the presence of this last-named communication. Two longitudinal vessels in the proboscidean sheath, never, however, extending any further than the œsophageal region, are perhaps only of secondary importance. I will henceforth call the individuals which are deprived of these vessels those of the first form, the others I will designate as the second form. (See the Explanation of the Plates.)

In the head we find two great lacunar spaces, one on each side of the proboscidian sheath (fig. 19). They fill up the head—before the ganglia—and have the proboscidian sheath between them. Besides these two lateral lacunæ one sometimes finds (not, however, seen by me in all the specimens) a broad and flattened lacuna above the proboscidian sheath, which has the whole width of the proboscidian sheath, but is tolerably flat in transverse sections, and which is temporarily separated from the other lacunæ by transverse muscular bands. In the tip of the snout the two lateral lacunæ communicate by an arch above the proboscidian sheath. When the lacunæ above the proboscidian sheath is present, it also opens in the above-mentioned arch. Further backwards this process is repeated just behind the supra-proboscidian commissure, and in front of the infra-proboscidian one. A broad arch is here situated above the proboscidian sheath. But between the two arches the lacuna above the proboscidian sheath has already had occasion here and there to mix its fluid contents with that

of the two lateral lacunæ, the transverse bands which separate them being here and there interrupted.

The two great lateral lacunæ are surrounded by a thin layer of transverse muscular fibres. Still, I am inclined to call these spaces "lacunæ," reserving the name of vessel for those that are in transverse section of a circular ellipsoidal shape. Bands of dorso-ventral muscles traverse the lacunæ, slanting backwards or forwards. They are so strongly inclined, that in transverse sections of  $\frac{1}{100}$  mm. I never saw a band from one wall to the other, but always found it cut off, so that in section they resembled finger-like protuberances from the walls. Bands which were twice cut through thus produced in sections an insular patch in the lacunæ. McIntosh gives a similar description of this arrangement in his "Great Canadian Carinella" (25).

As in *Cephalotrix*, I have here found a very thin layer of hyaline basal tissue, against which on the inner surface are found very distinct small round or ellipsoidal cells, with relatively large nuclei.

We now follow the lacunæ backwards. We have passed the supra-proboscidian commissure of the brain, and have seen that the supra-proboscidian lacuna, which occurs only in some individuals, is already coalesced with the other, and disappears.

Now, in those specimens which have a lacuna above the proboscidian sheath, there is also a lacuna below it. This, too, is wide and flattened, and becomes visible all at once, it evidently terminates blindly in front. The blind end lay in the same slice, wherein the infra-proboscidian commissure of the brain became visible. Close behind this region the innervation of the proboscis by two large nerve-trunks becomes visible. Just behind these the lacuna dilates, and then appears a broad arch (turned downwards) as a communication between these three lacunæ. This broad arch also is now and then traversed by large bands of transverse muscles.

It appears to me that all these transverse bands can co-



operate, and not in an insignificant manner, considerably to diminish the lumen of the lacunæ.

These two different types of communication of the lacunæ in the head I have described from specimens cut into transverse sections, but it would not surprise me if there are more types or variations, having found these two types in only four specimens. I must remark that these two types occur as well in the first form as in the second. (See the beginning of this description, p. 15.)

We now approach the œsophageal region. In those individuals where there is a large communication between the lacunæ of the head beneath the probiscidian sheath the mouth becomes visible when this lacuna disappears. The lacunæ, which down to this point have been situated on the sides of the probiscidian sheath, now descend to a level between the probiscidian sheath and intestine (figs. 19 and 20), as in *Cephalotrix* (fig. 21). They have not lost their circular fibres, and also preserve their inner investment of the thin hyaline basal layer, and the beautiful epithelium of little round cells, with relatively large nuclei. Still further backwards the lacunæ descend still further, and now lie on each side of the intestine, but so that their upper wall is just as high as the upper limit of the intestine.

In the œsophageal region I have to mention a peculiarity which, as far as I know, has not yet been seen in other forms. The lacunæ show numerous dorsal dilatations, a portion of which is separated from the bulk of the lacuna by a sometimes thin, sometimes large band. This band consists for the greater part of hyaline basal tissue, but some of the circular fibres also enter the band. I have represented it in figs. 2 and 4 diagrammatically. On the ventral border of the lacunæ arches, as indicated in the figure, only now and then occur. A transverse section through such a region is shown in the left half of fig. 23, and the more common case of arches directed upwards, in the right half of fig. 23 and in fig. 24. Rarely an arch directed upwards and one downwards were seen in the same section. In a younger specimen these separating bands

were more numerous in one and the same transverse section, but the bands were much thinner and the lacunæ reached lower down under the intestine than in an older specimen; but they never coalesced beneath the intestine.

In figs. 4 and 24 we still see two other thin longitudinal vessels in the œsophageal region. The form of *Carinella annulata*, where this occurs, I have called (see above) the second form. These two vessels lie in the proboscidian sheath. They terminate blindly in three of the four specimens examined, both in front and behind. They become visible gradually, not at once, and disappear also by degrees. In one of the specimens of the second form, I saw at the point where these vessels originate a trace of a communication of these vessels with the longitudinal blood-vessels, consisting in a pointed diverticulum of the blood-lacunæ towards the vessel in the proboscidian sheath, this point finishing in the hyaline basal layer of the proboscidian sheath, whilst the vessel of the sheath had not yet a lumen there, but only a little further behind. In a second specimen I noticed a space becoming visible above the horn of the semi-lunar section of the œsophagus, but lying within the œsophageal constrictor muscle. This space seemed to me to communicate with the vessel in the proboscidian sheath (the latter lying nearly on the same level as the horns of the œsophagus), and a few slices more forwards or backwards to communicate with the lateral blood lacuna. It is with due reserve that I mention this, the more so because I have seen this only on the right side of the animal, and never on the left.

I have stated that the two vessels in the proboscidian sheath lie on the same level as the two horns of the œsophagus. In the hindmost part I saw one of the vessels going down a little, approaching the median line which I have represented as seen from above in fig. 4. Similarly, with due reserve, I will mention what I have seen in a third specimen of the second form, of which I had only a small portion. Five times on the left side and twice on the right side, the vessel in the proboscidian sheath sent out a pointed diverticulum through the

muscular wall of the proboscidian sheath in a direction slanting downwards, the lacunæ doing so in the opposite direction, so that a connection between these two spaces may exist. In a slice which was very thick, the connection was complete, but the section was so thick that the whole canal, if it was one, lay in it. I have distinctly seen a lumen in it. The walls of this narrow canal were limited by fibres which were directed from the wall of the proboscidian sheath towards the walls of the blood-lacuna. Fig. 24 shows us a section through the œsophageal region of the second form.

In regard to the histological structure of these vessels I must be very brief. Sometimes both the epithelium layer and the hyaline basal layer of the proboscidian sheath, the latter being tolerably thick, covered them, so that the vessel cannot be said to lie in the lumen of the proboscidian sheath. Sometimes they were considerably swollen, and I saw neither hyaline basal layer nor epithelium layer covering them and separating them from the lumen of the proboscidian sheath. In such cases their wall was very thin, and their lumen divided into little compartments, more or less resembling certain portions of the nephridial system to be mentioned below. In both cases they lay upon the hyaline basal layer of the proboscidian sheath. Sometimes they were in no way of a peculiar colouring, sometimes they distinctly showed two colours, one part being extensively yellow. Of their cellular structure I can say nothing.

If nevertheless I were to make a hypothesis as to their possible physiological signification, I should be inclined to ask: Could they perhaps have any significance with respect to nutrition, oxygenation, &c., of the fluid of the proboscidian sheath? In this opinion I was strengthened when I noticed their probable connection with the vascular system, which, as we will soon see, communicates with the exterior by means of the nephridial system. This very provisional hypothesis will be further discussed in the description of the arrangements which we find in the following species.

Gradually going backwards we have now approached a region where the singular arches formed by the lacunæ

cease. This lacunar region I have called the œsophageal region. The blood-spaces have now changed their form into one which in transverse section is circular or ellipsoidal, so that now the name of vessels can be applied. Internally they are clothed with the cellular epithelium, next follows a hyaline basal layer and externally a layer of circular muscular fibres. I have nowhere observed a longitudinal layer of fibres. The region which follows the œsophageal one I will call the nephridial region, because we meet here with organs visibly belonging to that type of excretory apparatus of the Evertebrata, which Ray Lankester has united under the name of nephridia.

Above the blood-vessel, directly applied against it in a slanting direction, and only separated from it by a thin wall, lies a second large longitudinal canal, the nephridial canal (see figs. 4, 25, 26, 27). Its walls are similar to those of the blood-vessels. Thus the thin wall that separates them consists of five layers: epithelium, hyaline basal tissue, circular muscular fibres, hyaline basal tissue, epithelium. Indeed, a highly primitive nephridium, which is, as it were, a part of the blood-vessel separated from it! Now, in the whole nephridial region a spongy organ lies in the blood-vessel, placed on its outer wall, of which to my regret I could not make out sufficient histological details, at least none which I would venture to communicate as yet. This organ, which presents itself as a spongy gland, I will call the nephridial gland (see figs. 4, 25 to the left and to the right, and fig. 26 to the right). The nephridial canal has at its front end an open communication with the blood-vessel (see fig. 4 and fig. 25 on the right). Also at the other end where its lumen gradually becomes smaller (see fig. 4 and fig. 26 to the left). The nephridial canal further at intervals has open communications with the nephridial gland (see fig. 4 and fig. 25 on the left, and fig. 26 on the right). The lumen or the lumina of this gland are always separated from the lumen of the blood-vessel by a very thin wall. I have clearly noticed two excretory ducts, one on each side, by which the lumen of the nephridial canal communicates directly with the exterior, consequently also



that of the vascular system (see figs. 4, 24).<sup>1</sup> These excretory ducts lie above the lateral nerves. The epithelial layer and the hyaline basal layer clothe the whole duct. The epithelial layer passes gradually into that of the skin. The hyaline basal layer coalesces with the basal membrane of the skin, which deviates outwards, and the layer of circular fibres passes into that same layer which lies within the basal membrane. The whole is remarkable as bearing a very primitive character. The skin shows in the living animal a hardly perceptible cup-shaped deepening. In a transverse section this is seen to correspond with the outer infundibulum of the duct.

Behind the nephridial region I have followed the vascular system much further. The vessels in the intestinal region lie sometimes beneath, sometimes above the level of the lateral nerves (figs. 21, 22), are large and wide, and their wall again consists of the three layers already described. Here, too, I searched in vain for an exterior layer of longitudinal fibres to the vessel.

I have not had occasion to observe the connection of the two vessels in the posterior extremity of the animal.

### 3. *Carinoma Armandi* (McInt.), Oud.; figs. 5, 28—37, 56—61, 72—75.

Of this species the vascular system, neglecting a few smaller vessels, consists of four large lacunæ in the head, which communicate in the tip of the snout, and form two lacunæ in the cephalic region, passing into six longitudinal vessels further backwards, two of which are situated in the proboscidian sheath, terminating blindly behind two others above and outside of the proboscidian sheath, which also terminate blindly behind, whilst two others, which extend along the whole length

<sup>1</sup> Inducement to search for the nephridia of *Carinella*, unknown till to-day, and to hope to find a communication with the vascular system, was given me when Professor Hubrecht communicated to me that he had met with nephridia in two genera closely related to *Carinella* (the still inedited genus *Carinina* dredged by the "Challenger," and *Valencinia Armandi*, McInt.), and that he had succeeded in finding in the latter the internal and direct communication of the nephridium with the vascular system.

of the body, remain beneath the level of the nerve trunks, and finally communicate in the tail.

In the tip of the snout, already in the third section, where the thickness of the sections is about  $\frac{1}{70}$  mm., the communication of the lacunæ (fig. 28) is visible. A few sections further the spacious lacuna is already traversed by vertical bands, extremely thin, consisting of transverse muscular fibres, which again diverge amidst the tissue that surrounds the lacuna. In the thirteenth section the lumen of the proboscidian sheath penetrates between these lacunæ, and is situated in the axial line, but with one of the lacunæ above it. The two lacunar spaces on the sides of the proboscidian sheath gradually lose their thin bands, whilst they become divided, each by a broad vertical band (fig. 29). The lacuna above the proboscidian sheath becomes gradually flatter (seen in transverse sections, not marked in fig. 29), and is at every moment, sometimes to the left sometimes to the right, in connection with the lacunæ on the sides of the proboscidian sheath, sometimes even with both of them at once. In the meantime a thick, circular, muscular layer is formed, surrounding all the lacunæ, the contractions of which may aid in driving the fluid backwards. The circular muscular layer is closed entirely, and not, as asserts McIntosh, half open on its sides. Within this circular layer longitudinal fibres become visible, as well lining the four lacunæ as further backwards, between the fibres of the transverse bands which separate them. In this species, too, the fibres are not directly bathed by the fluid. Here and there the epithelium was visible very distinctly; it has the same character as that of the foregoing species, consisting of little round cells with relatively large nuclei. A little before the brain-ring the two lacunæ on each side of the proboscidian sheath coalesce into one, so that when they pass through the brain-ring only one great lacuna lies on each side of the proboscidian sheath. Just before the upper brain-commissure the broad band of circular muscular fibres diminishes so suddenly that one is inclined to think it disappears there. The same is seen when the brain-masses

and the lower brain-commissure become visible laterally and ventrally. By a more accurate contemplation with objectives of higher power, it can, however, be demonstrated that the circular muscular layer, which now consists of only a very few fibres, passes through the brain-ring at the same time with the lacunæ and the proboscidian sheath, whilst the number of longitudinal fibres has increased remarkably; and this circular muscular layer is the same which, behind the ganglia, will enclose the œsophagus, and thus is the same as the circular muscular layer of the body wall. The longitudinal fibres will form the layer of longitudinal muscular fibres, so that the circular layer which surrounds the lacunæ in the head of *Carinoma* is in no case comparable with the transverse fibrillar layer which surrounds the lacunæ in the head and other blood-spaces in *Carinella*. In the lacunæ of *Carinoma*, however, I have found the same hyaline basal layer and the same epithelium cells as in *Carinella*.

Immediately behind the ganglia the lacunæ grow downwards, but both are divided by a common horizontal band of transverse muscular fibres. The upper lacuna is the larger, and lies on the side of the proboscidian sheath, slanting downwards. The lower, or smaller, lies beneath the proboscidian sheath, and both of them between the two brain-masses. The broad band that separates the upper lacunæ from the lower consists of muscular fibres, which run from the left to the right, these fibres passing amongst those of the circular muscular layers. The two lower lacunæ are separated by a broad vertical band of hyaline basal tissue, in which numerous vertical transverse muscular fibres are visible, in the upper portion passing into the horizontal band, and in the lower diverging into the third (outermost) layer of isolated muscular longitudinal bundles, which layer penetrates here more inwards than elsewhere. The horizontal band disappears soon, thus the four lacunæ again become only two, lying on each side of the proboscidian sheath. The mouth becomes visible, and presses the lacunæ still further from one another and upwards.

The two lacunæ now extend dorsally (figs. 31 and 58), and

the uppermost portion, which is bent outwards, is suddenly separated from the lacunæ by a portion of the gelatinous stroma that everywhere fills up the spaces between the different organs in the body of the Nemerteans (figs. 31 and 59). Thus there are now formed four lacunar spaces. McIntosh has not seen this connection between the four blood-spaces. These two supra-proboscidian sheath-vessels soon obtain a distinct hyaline basal layer and an epithelium (fig. 73), and extend to the nephridial region, where they terminate blindly. I have seen no other communications with the blood-vessels of these two supra-proboscidian sheath-vessels.

Though they were very variable, and appeared to be subject to immense dilatation or contraction, they had, besides the two layers noted, no third layer of circular or longitudinal fibres. Their situation through the whole œsophageal region was the same laterally above the proboscidian sheath. Once I saw the left vessel extraordinarily dilated; once the right one divided into two, but sixty slices further these again merged into one (figs. 72 and 73). The blind end appears gradually, not abruptly.

We have seen that in *Carinella* there is a tendency in the œsophageal region of the longitudinal blood-spaces to give off arch-shaped portions directed upwards. If we suppose a similar separation to have taken place along the whole length of the vessel in the œsophageal region, then we have the two supra-proboscidian-sheath-vessels of the genus *Carinoma*. (Compare the fig. 4 with 5, and 24 with 32.)

In the same vertical section, where the two supra-proboscidian-sheath-vessels spring from the two great lacunæ, I saw very clearly on the left side—on the right side only a tendency to it was visible—how the left vessel in the proboscidian sheath communicates with the lacuna. I have therefore exactly figured the left half in figs. 58—61 of four subsequent slices.

Let us now call to mind for a moment what I have mentioned, with due reserve, of what I have seen in the second specimens of the second form (see p. 18), and let us then compare fig. 59. The band of transverse fibres, which sepa-



rates the larger lumen from the neighbouring smaller one, passes upwards into the circular layer of the proboscidian sheath, and below it surrounds the œsophagus. It thus proves to be the constrictor muscle of the œsophagus, and the smaller lumen lies within this constrictor, the same as I have seen in *Carinella*.

On the right side I only saw a similar communication between the vessel in the proboscidian sheath and the lumen within the œsophageal constrictor faintly indicated; but a connection between this and the great lumen I have not seen. McIntosh says that the two vessels in the proboscidian sheath have no connection with the blood-vessels anywhere. It is thus probable that this connection disappears when the animal becomes older, or that it only appears when the animal has reached a certain age; this only is sure, I have seen the connection. These two vessels are not very long. In the specimen I have examined, they are about one fifth of the œsophageal region. They terminated blindly, but not as in *Carinella*, gradually, but at once. Perhaps this is to be ascribed to the posterior end being filled with fluid or not. In regard to the histological structure, I cannot mention more than that they are invested on the inner side with the same layer of small cells as the blood-vessels and the proboscidian sheath; that their hyaline basal layer sometimes passes into that of the proboscidian sheath, sometimes is separated from it by the same cells, and that the epithelium layer of the proboscidian sheath always covered the vessels on their outside.

We now return to the region of the mouth, to the two great lacunæ with which the four last mentioned vessels are connected. These two great lacunæ, seven slices further backwards, are already surrounded by a circular layer of muscular fibres. This circular layer is well developed. A few slices further backwards the circular layer becomes thinner and thinner, but it still exists. Not before the midst of the œsophageal region some longitudinal fibres become visible outside of the circular, which are also not very sharply limited there. An immersion objective very soon showed that they

possess a very primitive character. After a few efforts, I succeeded in finding a very beautiful section through the longitudinal vessel, which section, being cut partly at an angle, furnished a very good picture of the two layers, which, as we see in fig. 74, have a thickness of only two or three cells, and consists of cells which have not yet lost their protoplasmatic character, and nevertheless give rise to a distinct fibre. Especially an isolated cell on the right side of the figure shows which cells give rise to the outermost investment of the blood-vessels. A whole section through a vessel and vertical section I have figured in fig. 75. This section lay just before the nephridial region, to which we will pass immediately, after having mentioned that the two great vessels that take their course from the level of the mouth till far behind, are always provided with a well-developed hyaline basal layer, and an epithelium with large nuclei (see figs. 74 and 75); and that in contracted portions of the vessels the basal layer forms protuberances towards the lumen, so regularly arranged that the whole has the appearance of a saw. These must be longitudinal folds lying side by side.

Only a very few sections (four in this specimen) before we see a true nephridial canal, we see that the lower portion of the blood-vessel changes its structure. A portion of its wall now is lined by palisade-shaped cells, regularly placed by the side of each other. We soon see a section in which a furrow pierces this changed wall-portion, and in the following slice we see this furrow cut off from the vessel by similar cells, and the nephridial canal is ready. There is thus an open anterior communication between the nephridial and the vascular system. The blood-vessel retains this changed ventral wall from section 718 to section 768. The nephridial canal, once separate, remains small when compared to the vessel, and lies next to it. Here and there I distinctly saw cilia, which were so long that they touched the opposite wall of the canal. A little further backwards we see the nephridial canal again in connection with the blood-vessel (see figs. 5 and 57: the communication took place in slice No. 762). At first, behind this connection the

canal becomes larger, also the cells, the nuclei in their base, and the cilia at their top. By-and-by it moves away from the vessel, descends, and finally is partly situated in the longitudinal muscular layer (fig. 33). A little further backwards a second canal suddenly appears on the side of the vessel, which soon divides into two canals, the upmost of which gradually goes upwards till above the level of the nerve-stems, then goes to the periphery, piercing the basilar membrane and the skin, and communicates with the exterior. The second undermost canal of the two coalesces further backwards with the chief canal beneath the blood-vessel. It is thus a branch which, rising from a certain branch of the nephridial canal, goes forwards, then a little backwards, and communicates with the exterior above the nerve-trunk (see fig. 5: fig. 34 is an ideal transverse section cut along the dotted line in fig. 5). There are thus a few slices which show six cut canals, on each side three, then a larger number with four canals (fig. 35). This point of rising of the branch we see in fig. 36. Still further backwards the canal again lies close to the vessel, and is finally connected with it (figs. 5 and 37), thus forming the hindmost open communication with the vascular system.

Let us now compare the nephridial system of *Carinoma* with that of *Carinella*. We find a striking resemblance in their design, but an extraordinary progress in the structure of that of the former. Both have in front and behind an open communication with the blood-vessel, both have one single excretory duct on each side, which rises from the hindmost part of the nephridial canal, goes directly outwards in *Carinella*, and in *Carinoma* first tends forwards a little before communicating with the exterior. Both have the excretory ducts lying above the nerve-stems. In *Carinella* the nephridial canal has occasion to communicate from time to time with the nephridial gland, which lies in the blood-vessel; in *Carinoma* it is connected in its whole course once with the blood-vessel, thus forming a third direct communication. The nephridial gland is absent in *Carinoma*, but we may perhaps suggest that its function has passed over to the cells of the



wall of the canal itself. Its cells have a typical glandular structure and design. A transverse section through the nephridial canal shows, in regard to the form and habitus of the cells (without their cilia), a perfect resemblance to all glandular ducts or glands of the stomach or other glands. The nephridial canal has more the appearance of a blood-vessel, with the same histological structure as the blood-vessel lying next to it, and thus probably serves as a reservoir for the materials excreted from the blood by the nephridial gland. In *Carinella*, cilia were absent; but a circular muscle layer surrounded the nephridial canal. In *Carinoma*, cilia are present, even in the extremity of the excretory duct; but the layer of circular muscular fibres is absent. All the cilia are directed outwards. In *Carinoma*, too, the excretory duct has the appearance of having progressed outwards, for the basal membrane, and even a small part of the circular muscular layer inside of it, are pressed outwards, as in *Carinella*. As far as close to the surface the duct is invested with its epithelium, and only at the rim of the opening there are cells that are intermediate between skin epithelium cells and nephridium glandular cells. Thus, the structure indicates that the nephridial system of *Carinoma* has a higher development than that of *Carinella*.

I have examined only a few sections behind this region, the body being still several centimetres longer. The blood-vessels do not show anything peculiar. In the tail their communication is very peculiar. They can indeed be followed till nearly to the tip of the tail, where, however, they do not coalesce directly but gradually increase in size, becoming lacunæ which communicate above the proctodæum. But anteriorly to this connection already many lacunæ, for the most part also above the intestine have become visible, which communicate from time to time with the vessels themselves, forming thus rudimentary transverse contracting vessels! It is very probable that these lacunæ also communicate with one another. Laterally to the vessels I have also seen lacunar spaces, but I could not find any communication, either with the vessels, or



with the blood-lacunæ, or with the exterior. Perhaps they are genital spaces.

4. *Valencinia longirostris*, Quatref. Figs. 13—16,  
41, 45—47, 50—55, 63, 67.

The vascular system of *Valencinia longirostris* resembles in the head that of *Carinoma Armandi*, consisting of longitudinal lacunæ which coalesce into two, when passing through the cerebral ring. But for the rest its principal traits are also common to all *Schizonemertea* and *Polia*. There is a median dorsal vessel, which lies in the œsophageal region in the proboscidian sheath, and behind it between the proboscidian sheath and the intestine. It communicates with the lacunæ above the inferior brain-commissure and it leaves the proboscidian sheath towards the hindmost part of the œsophageal region. This region is characterised by two peculiarities, (1) the whole œsophagus is surrounded by lacunæ with the exception of that portion which lies close to the proboscidian sheath, and (2), this region is the seat of the nephridial system. Behind this region two lacunæ are still visible at the sides of the proboscidian sheath, above the foremost half of the intestinal tract. Beneath the intestine we find two vessels, so that on a transverse section we see five blood-canals, of which three have muscular walls and two not. These five blood-spaces are united together by transverse vessels. The hindmost half of the intestinal region only shows three vessels, the lacunæ next to the proboscidian sheath having disappeared. Here, too, transverse vessels are present. All the transverse vessels lie above the diverticula of the intestine. The communication of the three longitudinal vessels takes place in the tail before the anal commissure of the nerve-trunks and both lie above the rectum.

A series of transverse sections of *Valencinia*, when examined from head to tail, shows in the tip of the snout (in my specimen in the ninth section) the beginning of the circular muscular layer in the shape of a small curve with its convexity

directed upwards; a few sections further backwards this little arch becomes larger, sending two horns downwards; again, a few sections further and the circular muscular layer is closed. Meanwhile we see within the little arch the beginnings of the lacunæ, for there are more than one, all situated against the circular layer, so that when this is closed there is also a circular arrangement of the lacunæ, which of course are all more or less triangular, with their bases against the circular layer and with their tops turned towards the centre (fig. 53). The lacunæ are separated from one another by transverse muscular fibres, which not only take their course from the one side of the circular layer to the other, so that they form in the centre a median chord, transversing each other in all directions, but which also extend further outwards than the circular layer, so that they appear to run radially from the centre to the skin. I seldom saw any communication between the lacunæ whenever a transverse band was partly absent. As in *Carinoma* longitudinal muscular fibres also took part in the limitation of these lacunæ, being placed both against the circular layer and against the transverse muscular bands, and also in the angles of the triangular lacunæ. Even between the transverse fibres of the bands, as in *Carinoma*, longitudinal fibres occurred. However, the blood did not directly bathe these fibres, but was separated from them by a richly developed beautiful epithelium of small round cells with relatively large granular nuclei as in *Carinoma*. On a sagittal section (fig. 67) going from above downwards we find the circular muscular layer (not indicated in the figure), a few longitudinal fibres, epithelium, lacuna, epithelium, longitudinal fibres, then the chord or cylinder of transverse fibres, and then the same arrangement in inverse order.

Where the epithelium cells were present in large numbers, the very thin and nearly colourless hyaline basal layer was not visible. It was clearly seen where the epithelium was torn off.

Though we cannot say that in *Carinoma* the opening of the proboscidian sheath is not wholly terminal, yet in *Valen-*

cinia it is placed still further backwards. In my specimen it becomes first visible in the fifty-sixth section, thus nearly on 1 mm. from the tip of the snout (in the preserved specimen), goes upwards till it reaches the circular muscular layer, and penetrates this a few slices further backwards, finally remaining in the centre of this ring-shaped layer. When the proboscidian sheath first touches the circular muscular layer the number of the lacunæ diminish by communicating with one another, and deviate more from the median line; but after the circular layer has given a passage to the sheath and has enclosed it, the number of the lacunæ is diminished to two, lying on the sides of the proboscidian sheath. There is no lacuna above the latter. One may thus say that in *Valencinia* the lacunæ in the head communicate not directly above the proboscidian sheath but indirectly. The brain-commissures now become visible, and the circular layer, the longitudinal fibres, the lacunæ and the proboscidian sheath protrude, as in *Carinoma*, through the cerebral ring. The lower half of the cerebral ring being very thick is seen in many slices. In the hindmost three sections, where it was visible, the two lacunæ slant downwards, and the fibres of the proboscidian sheath cut off a part of the left lacuna and enclose it between them. (Fig. 54, referring to *Lineus sanguineus*, may also serve for this species.) I believe this is abnormal, for in all Nemerteans where this process takes place, and which I examined also on transverse sections, both the lacunæ, except in two other cases, participated in this process. For the moment we leave the dorsal vessel in the proboscidian sheath, only pointing out that here as in *Carinoma*, a part of the lacunæ as it were penetrates the muscular wall of the proboscidian sheath, and extends further backwards as a vessel in the latter. This process I have also been able to follow in sagittal sections.

The lacunæ again remove to the sides of the proboscidian sheath. Now, beneath the latter a lacuna becomes visible, which terminates blindly in front, and in a following section is broad and flattened and thus may be compared with the "infra-

proboscidian channel" of McIntosh (26) (better "infra-proboscidian-sheath-channel"). It is separated from the two others and from the sheath by a horizontal broad band of transverse fibres (cf. *Carinoma*).

The next section shows us six lacunæ, for each of the three lacunæ is divided into two by transverse fibres, viz. the lacunæ on the sides of the proboscidian sheath are divided into an upper and a lower one, whilst that beneath the sheath into one right and left.

A little further backwards the transverse bands in the lacunæ on the sides of the proboscidian sheath disappear, and so we have again four lacunæ, one on each side of the sheath, and two beneath it, just as in *Carinoma*.

At the same time we see on each side a great ganglionic mass penetrating the circular layer. These are the posterior lobes (brain respirators). As soon as they are within the circular layer they are surrounded by a thin lacunar space, thus they are bathed (McIntosh) by a lacuna. These lacunæ as soon as the posterior lobes disappear, immediately unite with the two lacunæ beneath the proboscidian sheath, which in the meanwhile have moved from one another.

Besides the two brain respirators, still two smaller club-shaped ganglionic masses penetrate into the two lacunæ on the sides of the proboscidian sheath (are they brain processes?).

The two lacunæ on the sides of the sheath are wholly separated from the other lacunæ, even from those in which the two posterior lobes bathe, by the above mentioned horizontal band of transverse muscular fibres. After the disappearance of the lobes this band also disappears and the four lacunæ now coalesce into two.

This coalescence, however, is of very short duration, for they are again divided by transverse bands. The mouth becomes visible. The circular muscular layer in its lower portion is interrupted, deviates outwards, and finally encloses the œsophagus. The lacunæ and the longitudinal muscular layer, which always remain against the inner side of the circular layer, do the same as the circular layer (fig. 50), so that as



soon as the œsophagus is inclosed by the circular layer, it is at the same time surrounded by the longitudinal muscular layer and the lacunæ (fig. 51). The small transverse bands which continue to divide the lacunæ, are also present round the œsophagus and keep it connected with the circular layer, at an almost equal distance all round, of course not on its dorsal side where the proboscidian sheath lies, which is at the same time the cause, that on its sides through the whole length of the œsophageal region, a lacuna is visible, larger than the others. I shall call them proboscidian sheath lacunæ.

I have carefully examined all the little transverse bands of a small portion of the œsophageal region, with respect to their width and situation, but did not find any indication of metamerism or segmentation, so distinctly expressed behind the œsophageal region, both in the intestine as well as in the vascular system.

In the specimen examined the lacunar or œsophageal region took up nearly one third of the whole length of the animal. The lacunæ in the hindmost part of this region become gradually larger, at the same time diminishing in number, especially ventrally.

In this region, at the same time, a little more forwards the vessel in the proboscidian sheath penetrates through the wall of the sheath, and now lies below it, but so closely against it that I could not distinguish the two muscular layers, for the vessel too has now a very thin circular muscular layer. Also the intestine lies so closely against the blood-vessel that no space is seen between them. The process takes place within five slices, and it appears as if the circular layer of the proboscidian sheath moved upwards from below.

The median vessel, when lying in the sheath, shows an inner epithelium layer of the same cells which everywhere limit blood-spaces; then follows a hyaline basal layer. It always lay above the epithelium layer of the sheath, and the dorsal half of the wall of the vessel had quite another histological character than the ventral half. The layer outside the hyaline basal layer showed on the dorsal half glandular cells, as if the

median vessel in the proboscidian sheath has, as I suggested from the two vessels in the sheath of *Carinella* and *Carinoma*, some important bearing on the material interchange of the fluid in the proboscidian sheath. In accordance with this view the hyaline basal layer of the dorsal half is thin, of the ventral one thick. I further saw (see above) that in *Carinella* they were sometimes swollen and spongy. Their surface was thus enlarged. In *Carinoma* I have never seen them so swollen, but here too their surface was on all sides surrounded by the fluid of the sheath, because their attachment on the inner surface of the sheath only takes place along a very small base; whilst in *Valencinia* the vessel is not only lifted up and supported by little bands, but is also washed on its ventral surface by the fluid of the proboscidian sheath. The preparations, however, were not sufficiently preserved to give a representation of it. In sagittal sections I have also seen the median vessel leave the proboscidian sheath.

In this region the lacunæ, as we have mentioned above, diminish in number, especially ventrally. However, not all the ventral lacunæ disappear. The intestine shows here, on the sides of the median line, an inward fold, in which a lacuna remains visible, which further backwards obtains a layer of circular muscular fibres, so that finally these lacunæ have become vessels. Not so the proboscidian lacunæ, with which all the remaining lacunæ have gradually coalesced. They remain running, on the sides of the proboscidian sheath, without muscular or fibrillar walls, through the whole foremost half of the intestinal region. Now and then they seem to be lined with fibres, but on closer examination these prove to be only transverse bands, which temporarily only limit them on their upper or lower side. They disappear as soon as they have come.

In the foremost half of the intestinal region thus there are five longitudinal blood-spaces. These are united together by transverse vessels, which are extremely thin, and run regularly over each diverticulum (figs. 14, 15, 52). These transverse vessels I have seen both in transverse and in sagittal sections,

but in none of my preparations did I see circular fibres surrounding them, only a thin hyaline basal layer, and occasionally epithelium. They stuck, as it were, to the diverticula; their wall, at the same time, was the wall of the intestine.

In the hindmost half of the intestinal region the lacunar spaces of the sides of the proboscidian sheath are absent. They have gradually disappeared (fig. 15), and now only three longitudinal vessels occur (figs. 16, 41) with their transverse vessels, which are visible down to the hindmost communication of the three longitudinal vessels above the proctodæum; sometimes this latter communication is invisible.

The lacunæ surrounding the œsophagus and the two long lacunar spaces next to the proboscidian sheath in the foremost half of the intestinal region are always internally limited by the epithelium cells already mentioned; externally by an extremely thin hyaline basal layer. In the dorsal vessel, as soon as it lies beneath the proboscidian sheath outside the hyaline basal layer, a thick layer of circular muscular fibres are seen; also in the two ventral vessels. In vain did I look for longitudinal fibres. The two ventral vessels lay in a fold, turned inwards, of the intestine amidst a gelatinous stroma that filled up this fold. This stroma has a radiating arrangement round the vessel. Probably these rays are local thickenings arising from the violent contraction of the vessel. In the stroma great granular nuclei were visible. The whole looked almost like fig. 63.

Let us now, with respect to the vascular system, compare *Valencinia* with *Carinoma* and *Carinella*. We have seen that *Carinoma* in its head (except in the arrangement of the lacunæ) greatly resembles *Valencinia*, and that the remaining body bears a likeness to that of *Carinella*, with some differences in the œsophageal region and in the nephridial system. Both in *Carinoma* and *Carinella* there is an œsophageal region which differs from the rest of the body by the blood-spaces in this region having here a strong tendency to detach from themselves portions (*Carinella*), or have even already finished this process (*Carinoma*), especially *Cari-*



nella, shows on transverse sections in its blood lacunæ something indefinite, and the lacunæ sometimes go down very far beneath the intestine. As to Valencinia, if we are in a region where the lacunæ have not yet wholly surrounded the œsophagus, we are struck by the resemblance of the situation and habitus of the lacunæ with those of Carinella. Moreover, we are inclined to compare the arches of the lacunar spaces in Carinella, and the supra-proboscidian sheath-vessels in Carinoma with the proboscidian sheath lacunæ of Valencinia, for they are all separated portions of the blood-vessels, which have moved upwards, and are placed next to the proboscidian sheath; and they are all in direct communication with the vascular system. The different situation which they seem to have in Carinoma and Valencinia may not be of importance. In Valencinia they lie within the longitudinal muscular layer, and in Carinoma they appear to lie in the longitudinal layer—but I say they appear, for, properly speaking, they lie also within this layer, but their high triangular shape makes it appear as if they were placed between the fibres of this layer. Further backwards they lose their triangular shape, descend to a lower place, and in habitus and situation more resemble the proboscidian sheath lacunæ of Valencinia. In Valencinia the intestine is comparatively large, and the blood-vessels lie beneath it; in Carinoma the intestine is comparatively small, and the blood-vessels lie next to it.

Let us now compare the two vessels in the proboscidian sheath in Carinella and Carinoma with the median dorsal vessel of Valencinia. Suppose that the points of origin of the two vessels in the two former are moved forwards, and at the same time approach the median line, and even reach this, so that they coalesce, then there is no reason that two proboscidian sheath-vessels will be formed. Only one will be formed, viz. a median dorsal vessel, lying in the median line, and at the bottom of the proboscidian sheath, and communicating with the two great lacunæ on the sides of the sheath, which now, in accordance with this simpler origin of the median vessel, will temporarily reach one another beneath the



proboscidian sheath, as is the case in *Valencinia*. If the two lacunæ become vessels, then we have a bidentate fork, a pitchfork, and we have the form that occurs in all the *Hoplonemertea*. The median dorsal vessel will, however, not go farther than the œsophageal region in the proboscidian sheath as in *Carinella* and *Valencinia*, and several higher forms mentioned hereafter; and suppose now that from the point where it finishes a groove is formed by the proboscidian sheath down its whole length, communicating with the vessel in the sheath, and is now cut off, then we have the median dorsal vessel of all the *Schizonemertea* and *Hoplone-mertea*. Simultaneously with the formation of diverticula on the intestine, there are formed transverse vessels over these diverticula between the longitudinal vessels.

The reason that I do not treat the nephridial system at the same time with the vascular system is that I have nowhere seen open or direct communication between these two systems.

The nephridial system is situated on the sides of the œsophagus, in the lacunar spaces between œsophagus and longitudinal muscular layer, and against the latter. It consists (and this is very plainly visible on sagittal sections) of two longitudinal canals, which are united by transverse canals, just like a ladder. The foremost part was about one mm. from the hindmost point of the opening of the mouth, the hindmost part a little before the point where the median vessel leaves the proboscidian sheath. The whole length was fifteen mm. in a specimen of four cm. in length (in spirits).

The nephridial system in *Valencinia* offers us an important peculiarity, viz. there are more than one pair of excretory ducts. I have found in the specimen cut in transverse sections twenty-six pairs of excretory ducts, all lying above the nerve-trunks, nearly touching them. The slices in which I found them were the following :

On the Left.						On the Right.
277	.	.	.	.	.	305
361	.	.	.	.	.	336
421	.	.	.	.	.	423
452	.	.	.	.	.	462
493	.	.	.	.	.	517
554	.	.	.	.	.	533
599	.	.	.	.	.	603
623	.	.	.	.	.	620
638	.	.	.	.	.	651
662	.	.	.	.	.	671
684	.	.	.	.	.	700
697	.	.	.	.	.	711
719	.	.	.	.	.	722
736	.	.	.	.	.	738
744	.	.	.	.	.	752
765	.	.	.	.	.	765
776	.	.	.	.	Right side damaged.	
803	.	.	.	.	.	803
838	.	.	.	.	.	814
874	.	.	.	.	Right side damaged.	
885	.	.	.	.	.	885
912	.	.	.	.	.	903
959	.	.	.	.	.	972
1010	.	.	.	.	.	1021
1057	.	.	.	.	.	1052
1070	.	.	.	.	.	1070
?	.	.	.	.	.	1090

Probably the ducts run quite straight outwards ; this was to be seen especially in regard to the very small hindmost ducts, whilst the foremost, which were much larger, sometimes ran obliquely forwards, sometimes backwards, or were curved. Some of them had a small lumen, others a lumen which was visible through many sections, and locally dilated. As a rule, the ducts were smaller as they lay further backwards. If we reflect that the numbers I have given of the slices are those in which I at first saw anything of a duct, either its beginning, or aperture, or the knee of a crooked duct, then some irregularities in the arrangement of the ducts are already explained. But let us take for a moment the two most remote

ducts of one pair, e.g., 277 and 305, or 361 and 366, which are removed twenty and twenty-four sections from one another; and if we now know that sixty-six sections form 1 mm., then we see that these ducts were removed only between  $\frac{1}{3}$  and  $\frac{1}{4} = \frac{7}{24}$  of a millimetre from one another. And we may conclude that such irregularities are the results of the high contractility of such worms as Nemerteans. If we reflect on all these causes, it is indeed striking how the ducts are arranged by pairs.

The canals themselves in the transverse sections were very faintly coloured, and in the beginning I did not see them, not in any way thinking of a water-vascular system. (It was the first Nemertean I ever examined.) Already I had found and noticed more than one pair of ducts, and seen that they always began close to the inner longitudinal muscular coat, without comprehending their significance. It was Professor Hubrecht who not only drew my attention to the nephridial system, but who also decided as to the connection between these ducts and that system. When I had once observed this organ I saw it wherever it was present, and I immediately found even the smallest ducts of 4—6 mikrom. Shortly afterwards I could also very well see the connection of the ducts with the system of canals.

The ducts have a wall of one single row of palissade-shaped cells, with granular contents placed side by side, somewhat obliquely bent outwards. Each cell is provided with a cilium of up to 200 mikrom. in length. It may be remarked that the excretory ducts are all open towards the basal membrane, then suddenly narrow, as if the basal membrane contracts them. Outside the basal membrane they widen again, but here I rarely saw their lumen. Where it was visible I again saw large cilia, and the cells were still more granular, and their limits were not sharply visible and they were not so well coloured as the cells of the duct within the basal membrane. Although I saw distinctly in *Carinella* and *Carinoma* that the basal membrane was pressed outwards, in *Valencinia longirostris* I saw neither this nor the reverse. The basal membrane was

simply perforated, neither pointing towards the periphery nor inwards.

In a specimen, cut sagittally, the nephridial canals were better coloured, but neither in transverse nor in longitudinal sections could I observe cilia in the canals. On the sagittal sections I could not find any openings in the skin, but I did find the ducts within the basal membrane. If I have seen well, these ducts open into the upper longitudinal canal where a transverse canal also falls into it.

On these better coloured sagittal sections I saw that the canals have walls of one single row of cells, the nuclei of which, intensely coloured, lay on the bottom of the cells, as Von Kennel represents it, of *Notospermus* (*Cerebratulus*).

Already I have mentioned that the foremost ducts were wider and better developed than the hindmost, so that the first were easily found, the latter only with difficulty. It appears that with the growth of the animal also the œsophageal region grows, and probably preserves the same relative length to the whole body, e.g. one third of its total length. The nephridial system appears to grow gradually with the œsophageal region. We are further inclined to conclude, if we observe the difference between the foremost and hindmost ducts, that the foremost part of the œsophageal regions and thus also of the nephridial system, is the oldest, the hindmost the youngest.

At any rate *Valencinia* displays, not only in its diverticula of the intestine, in its transverse vessels and in its genital organs, a clear internal segmentation, but also in the œsophageal region a certain degree of metamerism is visible in the nephridial system, which is formed like two ladder-shaped systems on each side, having on the level of each step a pair of excretory ducts.

##### 5. *Polia curta*, Hubr. Figs. 11, 12, 43—51.

Two lacunæ in the head, which terminate blindly anteriorly, communicate above the proboscidian sheath, then beneath it, spread themselves over the brain, inclose the posterior lobes and



the œsophagus. There is a tendency to form five longitudinal blood-spaces. Behind the œsophageal region there are three vessels, united by transverse vessels. Communication of the three vessels occurs in the tail before the anal commissure, and like this, above the intestine. In the foremost half of the œsophageal region the median vessel lies in the proboscidian sheath. Its foremost communication is with the lacunæ above the lower brain-commissure.

In the head the vascular system becomes visible not at the tip of the snout but a little distance from it; in the specimen I examined, in the twenty-first slice, that is, about two-fifths mm. from the tip, the specimen had (in spirits) a width of one and a half, and a length of twenty-three mm. Quite in front there is no communication, two lacunæ becoming visible at once. They are flat (fig. 43). The circular muscular layer is already well formed dorsally and ventrally from the lacunæ. On the sides, however, the fibres cross one another and extend divergently in the surrounding tissue to the skin. A similar crossing of transverse fibres, but in a higher degree and number, also takes place in the middle of the area between the two layers of circular fibres, so that it appears as if the lacunæ lie in a transverse muscular band in the shape of an 8 (  $\infty$  ) lying sideways.

As the upper lobes protrude forwards and have on their foremost part the upper brain-commissure, which is very thick, we obtain a figure as if the lacunæ with the circular layer lie beneath the brain.

Behind the upper brain-commissure the brain on both sides increases in size, and the proboscidian sheath, which in the meantime has become visible, has penetrated the circular muscular layer, and taken up a position between the two lacunæ, and is gradually placed, with the lacunæ and the circular muscular layer, between the two brain-masses. Here is found the lower brain-commissure. Just before this becomes visible the lacunæ coalesce above the proboscidian sheath (fig. 44), and gradually spread over the brain. On both sides of the sheath two small lacunæ remain; these go

downwards, coalesce beneath the proboscidian sheath, communicate with the median dorsal vessel in the sheath, remain a moment in their places, and descend still further behind the lower brain commissure, to unite with the lacunæ, which have now totally enclosed the large posterior lobes, and seem to come from above, whilst the circular muscular layer, which has always followed all the movements of the lacunæ, now closes again (figs. 45, 46, 47, 48). A little further backwards the posterior lobes gradually become smaller, and two short diverticula of the œsophagus, directed forwards and terminating blindly, now become visible (figs. 49 and 50). What in *Valencinia* I saw only once I here saw continually, even on the lateral nerve trunks, viz. club-shaped ganglionic masses projecting into the lacunæ. Behind the mouth the lacunæ again coalesce and embrace the œsophagus, but next to the proboscidian sheath two distinct uninterrupted lacunar spaces are always visible (fig. 51). But these latter extend beyond the point where the median vessel leaves the proboscidian sheath, whilst already the number of the lacunæ round the œsophagus diminishes, and two lacunæ present themselves constantly at the same places beneath the intestine, so that we have here again a figure of five longitudinal blood-spaces. I have not seen in *Polia curta* that these five longitudinal blood-spaces are united by transverse vessels. At first, when the two proboscidian sheath lacunæ have disappeared, and thus when there are only three vessels, transverse uniting vessels become visible, one over each diverticulum. The communication of the three longitudinal vessels in the tail is the same as in *Valencinia*.

Just behind the lower brain-commissure the first longitudinal muscular fibres occur within the circular muscular coat. I have not seen a longitudinal fibre in the præcerebral region. This is very anomalous.

As to the internal coating of the lacunæ and vessels, it is the same as in *Valencinia*; also here the median dorsal vessel, when it lies in the proboscidian sheath, shows its dorsal side formed otherwise than its ventral arch; also here it is

held up by ligatures, of which the remotest on the left and right sides are the most solid; and also here from time to time lumina are distinctly visible beneath the vessel, and it appears that the proboscidian sheath fluid also bathes its ventral surface. In another specimen I saw a part of this vessel, quite at its commencement, still before the mouth, where it seems not to be as described above. I have represented it in fig. 68. The hyaline basal layer everywhere is the same as in *Valencinia*, but the vessels of *Polia* I have not observed to be surrounded by circular muscular fibres. In the median vessel beneath the proboscidian sheath I have seen out of the hyaline basal layer large nuclei in the gelatinous stroma, heaped up against the hyaline basal layer, just as is seen in fig. 65 of a transverse vessel in *Cerebratulus marginatus*. The two ventral vessels fill the whole space of the longitudinal grooves in the intestine and between it and the longitudinal muscular layer, so that the radially developed stroma, visible in *Valencinia* and *Langia* (figs. 62—64), was absent here, at least in the specimens examined by me. The dorsal vessel beneath the proboscidian sheath was pressed against the intestine, but not against the wall of the proboscidian sheath. There was a little stroma between them.

The nephridial system here is also situated in the œsophageal region. It commences near the mouth, and finishes when the first transverse vessel is seen; thus in a region where three longitudinal vessels are already present without lacunæ it penetrates even into the intestinal region.

I cannot say how it appears when viewed obliquely.

Openings and ducts of this system I found in the following slices :

Left.					Right.
125	.	.	.	.	125 ?
134 ?	.	.	.	.	135
145 ?	.	.	.	.	146
157	.	.	.	.	166
188	.	.	.	.	184
199	.	.	.	.	200
213	.	.	.	.	213
222	.	.	.	.	223
Nothing	.	.	.	.	231
285	.	.	.	.	Nothing.
290	.	.	.	.	294
309	.	.	.	.	310

The excretory ducts, as in all the foregoing species, are projected above the nerve stems, and, as in *Valencinia*, nearly touch them; but, as to their further course through the outer longitudinal muscular coat, I saw some running straight to the skin, some downwards, and others even very obliquely rising upwards.

The excretory ducts for the most part were well developed (probably I had a nearly full grown individual); some of them were extraordinarily enlarged, but all were contracted by the basal membrane and in the skin, so that the external opening was only a few mikromillimetres. The cells in the walls are smaller than those of *Valencinia*, and placed otherwise, not shaped like palisades but like a pavement, and not pressed against one another but apart. Their nuclei seen from the side were flat and rectilineal, and from above ellipsoidal; but all these appearances may be the results of a stretching of the outer muscular layer. The histological structure of the canals of the system is the typical one (cf. Von Kennel). I have not seen cilia in them, nor direct communication with the lacunar blood-spaces.

#### 6. *Lineus sanguineus* (Rathke), McInt., figs. 17, 18, 54.

In the main the same vascular system as *Polia curta*, except in the head, of which the lacunæ are arranged otherwise.



In all sections through the præcerebral region the lacuna is only one, horse-shoe shaped, having between its legs the proboscidian sheath, which become visible at the same time with this lacune. The circular muscular layer, the lacuna and the proboscidian sheath, I saw together in the sixth slice ( $\frac{1}{11}$  mm. from the tip of the snout). The former was present only on the dorsal side, and the fibres diverge on the sides, extending and diverging through the surrounding tissue nearly to the basal membrane. At first in the eighteenth slice the lower arch of the circular muscular layer presents itself, also diverging in the sides and thus crossing with its fibres those of the upper arch. So the proboscidian sheath in *Lineus* has not penetrated through the circular muscular layer, as in the other species, for it was already present when the lower arch of this layer formed itself. Already from the beginning I saw longitudinal fibres occurring within the circular muscular layer, as in *Valencinia* (see, however, Polia). Just before the upper brain commissure the lacunæ united beneath the proboscidian sheath, whilst they parted above it. The horseshoe is now turned, with its legs upwards. Now also it breaks beneath the sheath, forming thus two lacunæ, one on each side of the proboscidian sheath. The left of these (in my specimen) (fig. 54) communicates with the median vessel in the proboscidian sheath. But this I regard as absolutely abnormal. (In the two other specimens I examined, the proboscis much interfered with my observations of this process.) My specimen was greatly contracted, but it seems to me, that in general the region that follows closely resembles that same region in *Valencinia*, both with regard to the form and extent of the circular muscular layer, the longitudinal fibres, the transverse bands, lacunæ, proboscidian sheath, &c. Also with regard to the manner of embracing the posterior lobes and the œsophagus.

Better than in the two former species, the lacunæ on the sides of the proboscidian sheath remain visible. In transverse sections they are round, their hyaline basal layer well coloured, their epithelium well developed. They are separated from the

other lacunar spaces, especially in the foremost half of the œsophageal region, by transverse fibres, and only now and then communicate with the other lacunæ. At first in the hindmost half the separation is less distinct, they lose their vascular character and unite more with the other lacunæ. They always remain within the longitudinal muscular layer.

About the region where the median vessel leaves the proboscidian sheath, two ventral lacunæ become larger than the rest, and are always visible at the same point. A hundred slices further on there are some small lacunar spaces, but afterwards no more. These two lacunæ are the foremost portions of the ventral vessels. In the meanwhile the two proboscidian-sheath-lacunæ have disappeared, and the remaining lacunæ arrange themselves so that they bear a likeness to the rudiments of transverse vessels, so that I cannot precisely note where the foremost well-defined transverse vessel may be said to occur. When the first well-defined vessel is visible the two proboscidian sheath lacunæ have already disappeared. The rest is entirely similar to *Valencinia* and *Polia*.

The inner coating of the blood-spaces with the epithelium and the thin hyaline basal layer was everywhere the same. In none of the three specimens examined did the median vessel beneath the proboscidian sheath lie against the intestine or against the proboscidian sheath, but freely amidst the gelatinous stroma. Outside the hyaline basal layer, nuclei were grouped. The same is the case with the ventral vessels. From what I have seen further on in the intestinal region, I may state that they have only a thin layer of circular and a thick one of longitudinal fibres.

The dorsal vessel in the proboscidian sheath displays the same peculiarities which I mentioned in speaking of *Valencinia* and *Polia*.

The transverse vessels, as in *Valencinia*, were so closely attached to the wall of the intestinal diverticula that they appeared to have a common wall.

The situation of the nephridial system is the same as in *Valencinia* and *Polia*. To the left and to the right it lies

against the inner surface of the inner longitudinal muscular coat, and stretches no farther back than the dorsal vessel in the proboscidian sheath. The canals are very thin, with a very small lumen and relatively thick walls. Anteriorly the system does not reach the mouth. Also in *Lineus sanguineus* I found many more than one pair of excretory ducts.

I have only traced it in two specimens, an old one (X) and a young one (Y). All the excretory ducts lay above the nerve trunks in the sections here enumerated :

X.			Y.		
Closure of the Mouth-slit 210.			Closure of the Mouth-slit 75.		
Left side.		Right side.	Left side.		Right side.
228	.	240	99	.	Nothing.
?	.	309	121	.	121
341	.	325	Nothing	.	125
358	.	353	133	.	134
372 ?	.	373 ?	136	.	Nothing.
Nothing.	.	377 ?	143	.	Nothing.
405	.	404	147	.	146
419	.	415	153	.	Nothing.
437	.	437	The dorsal vessel leaves the proboscidian sheath in 155.		
447	.	446			
476	.	472			

The dorsal vessel leaves the proboscidian sheath in 479.

Also this observation points to the increase of the number of excretory ducts in proportion to the growth and age of the animal.

I could not see cilia in the canals. In *Lineus sanguineus*—at least in the two specimens examined by me—the excretory ducts were not so close to the lateral nerves. If we trace a horizontal line through the centrum of the transverse section of the body the nerve stems lie just beneath this line, and the excretory ducts of X lay at an angle of  $45^{\circ}$ , that of Y at an angle of  $5.10^{\circ}$  inclined against the horizontal line.

Though X was older than Y the excretory ducts of X were limited by smaller cells and less visible, that of Y by larger cells, contiguous, as in *Valencinia*, and immediately visible,

even with a glass of magnifying power of 30—40 times, having been better coloured (picro-carmin of Ranvier).

In neither of the two specimens were the excretory ducts open. They were sometimes filled by a granular secretion, so that I could not observe the cilia. Here I did not see any difference between the foremost and hindmost ducts. On observing the two lists one is inclined to conclude that they arise here irregularly, though always segmentally projected in pairs.

#### 7. *Lineus gesserensis* (O. F. M.), McInt.

Similar to the foregoing species, but the two proboscidian sheath lacunæ, even in the foremost part of the œsophageal region, are not so well separated by transverse bands from the remaining lacunæ.

The specimen, owing to the insufficient preservation of the microscopical slices, was not suitable for closer examination of the nephridial system.

#### 8. *Cerebratulus marginatus* (Ren.), fig. 65.

In the main resembling *Lineus sanguineus*.

The lacunæ, which go downwards to communicate with the dorsal vessel, first form a true vessel, which only a few sections further backwards penetrates the wall of the proboscidian sheath. More than elsewhere this vessel displays a different character in its upper and lower arch. The cells of the upper side are stretched, are situated against each other, and are fan-shaped in their arrangement. Next to the proboscidian sheath in the brain region lie two large lacunæ, separated from those that embrace the mouth by a horizontal transverse band of muscular fibres, as in *Lineus*. In these large lacunæ the posterior brain lobes bathe, which extend far backwards, even behind the slit of the mouth.

In another fragment, which belonged to the œsophageal region, but was situated further backwards, I saw, next to the proboscidian sheath, in the angle formed by its wall and the longitudinal muscular coat on both sides, a longitudinal vessel,



which resembled a blood-vessel. Once a transverse vessel ran from it to the circumference of the intestine, but as the sections were made only through the upper quarter of this region I cannot say anything more on the further course of this vessel.

Somewhat on one side of the upper half of the intestine I saw a second longitudinal vessel, which is undoubtedly a nephridial canal.

Over the intestinal diverticula transverse vessels run from the median vessel to the two ventral ones. Fig. 65 gives us a representation of a transverse section through such a transverse vessel, around which the surrounding stroma is radially folded, with numerous nuclei heaped in the immediate neighbourhood.

9. *Cerebratulus hepaticus*, Hubr., fig. 66, 69, very similar to *C. marginatus*.

In the head there are within the circular muscular layer three large lacunæ (one above the proboscidian sheath), separated from one another by two massive bundles of longitudinal muscular fibres. In the region of the cerebrum the longitudinal fibres have increased in number, lying against the circular muscular coat. The proboscidian sheath, at first lying against the lower arch, has removed towards the upper arch of the circular coat. The lacunæ have united to one, which is horse-shoe shaped, with its legs upwards. The lacuna communicates directly with the median vessel in the proboscidian sheath. Behind this section, some fibres of the circular layer of the proboscidian sheath to the left and to the right take their course downwards, very obliquely, however, so that they cross one another, and cut the horse-shoe shaped lacuna into three. The one lying beneath the proboscidian sheath is triangular with its top turned upwards. The circular muscular layer of the proboscidian sheath increases considerably, so that the lacunæ are pressed sideways, and the lower lacuna very far downwards. In the meanwhile the two lateral lacunæ embrace the posterior cerebral lobes, and the sides of the tri-

angular lower lacuna become gradually horizontal, forming a horizontal band, which separates the lateral lacunæ and the posterior lobes from the two smaller lower lacunæ (the one being now divided by vertical transverse muscular fibres into two). The mouth-slit becomes visible. The two lower lacunæ gradually slant downwards round the œsophagus, leaving behind in its folds from time to time small lacunæ. The two upper lacunæ gradually become very small, and, as the horizontal band has disappeared, they now lie on what may be called in the transverse section the two horns of the half-moon shaped intestine. The mouth-slit is now closed, and the œsophagus is, except the ventral side and the side towards the proboscidian sheath, surrounded by lacunæ. The upper surface of the median vessel in the proboscidian sheath again differs from the lower, rests upon the inner (longitudinal) layer of the sheath, is, however, not held up by small bands. It touches the wall of the sheath only along a very thin base (see fig. 69).

The part in which the nephridial system is situated was not represented in the series I examined. The part that follows now lies in the intestinal region. Generative organs could be detected. The median vessel lies beneath the proboscidian sheath, and not far from the median line, on the ventral side of the intestine, the two ventral vessels are visible. Sometimes transverse vessels were very plainly to be seen, opening into one of the three longitudinal ones.

From a section which was situated still further backwards, and very well preserved, I give a representation of one of the ventral vessels in fig. 66. The inner epithelial layer is distinctly visible, also the large hyaline basal layer, thickened here and there by contraction, and better coloured. Following upon this there is a distinct layer of circular fibres, but no longitudinal. The stroma is radially contracted. Some cells in the stroma have a very distinct protoplasmic aspect.

In a tail-portion transverse vessels were observed, even over the hindmost diverticulum.

10. *Cerebratulus urticans* (J. Müll), Hubr., fig. 48.

Quite at the tip of the snout there is only one lacuna. The proboscidian sheath lies beneath it. A circular muscular layer surrounds them. This layer is already formed on its dorsal part, when the lacuna and the proboscidian sheath become visible. So here, too, the proboscidian sheath does not penetrate a circular layer. Already, at the foremost part, longitudinal fibres are visible within the circular muscular coat, which in the meanwhile is closed. The proboscidian sheath rests on the ventral side of the circular layer. In the medial line dorsally a bundle of longitudinal fibres increase in number, and finally touch the proboscidian sheath, so that the lacuna is divided into two, one on each side of the proboscidian sheath. But we may as well say there are in the head of *C. urticans* two lacunæ, which communicate anteriorly by a broad arch above the proboscidian sheath, as occurs in so many Nemertea. A little further backwards the wall of the proboscidian sheath increases so that it pushes away the longitudinal bundle on its two sides, and touches the dorsal arch of the circular muscular layer. Now the lacunæ are each surrounded by longitudinal fibres. Immediately before the cerebral ring both the circular layers greatly diminish; one would not recognise them, especially that of the proboscidian sheath. The two lacunæ approach each other ventrally, finally unite, lying beneath the sheath. They communicate directly with the dorsal vessel in the sheath, but remain one single lacuna beneath the proboscidian sheath, between this and the lower brain-commissure. The proboscidian sheath again acquires a thicker circular layer. The upper arch of the medial vessel is again different from the lower. It is held up by a spongy tissue.

As soon as the lower brain-commissure has disappeared, the lacuna beneath the proboscidian sheath goes down still further, and acquires a trapezoidal figure, limited above by the sheath; to the left and right by the lower lobes (from which the lateral nerves arise), and beneath by the outer longitudinal muscular

coat. It is, as well as the proboscidian sheath, always surrounded by the two well-known muscular coats, sending, as it were, two branches between the proboscidian sheath and the brain masses; it next gradually embraces the posterior lobes (as in fig. 48).

The mouth then becomes visible and presses the circular muscular layer a little upwards. Transverse vertical muscular fibres appear between this layer and the proboscidian sheath, so that the lacuna is divided into two. These two lacunæ are again divided into four by a horizontal band of muscular fibres between the proboscidian sheath and the stomodæum.

The two lacunæ beneath the horizontal band will again embrace the stomodæum, leaving here and there little lacunæ. The two lacunæ above the band, after the disappearance of the posterior lobes, acquire a circular layer of muscular fibres and diminish in size. The lacunæ round the stomodæum here and there disappear, as if they terminated blindly; some of them are still to be recognised, but the only distinctly visible lacunæ are the above-mentioned two with a circular layer and next to the proboscidian sheath: *caetera desunt*. (Two heads have served for this description; there was no difference between them.)

### 11. *Cerebratulus roseus* (delle Ch.), Hubr.

The præcerebral region so strikingly resembles that of *Cer. urticans*, that I at first believed there was an error in the determination. As soon, however, as the circular muscular layer with its contents passes through the cerebral ring, differences are to be seen.

The two lacunæ on the sides of the proboscidian sheath unite beneath the sheath, but instead of communicating directly with the medial vessel, a part of the now single lacuna is cut off by the circular muscular fibres of the proboscidian sheath, so that a flat lacuna lies between this wall. This lacuna rises between the fibres, finally comes within the circular coat, and is now the median vessel. So that the median vessel here, as in *Cerebratulus marginatus*, goes further



forwards beneath the proboscidian sheath, and communicates indirectly with the lacunæ. For a few slices the great lacuna retains its horse-shoe shape. Then a horizontal band of transverse fibres divides the lacuna into three, two on the sides of the proboscidian sheath, and one beneath it. The lower brain-commissure is passed by, and the mouth becomes visible, and still the whole figure is the same. Now the two lacunæ next to the proboscidian sheath embrace the posterior lobes. The horizontal band is still present and also the lacuna beneath it. On the sides of this lacuna two others arise, which of course terminate blindly forwards. These three are separated by vertical muscular fibres, passing into those of the proboscidian sheath. So the area of the circular muscular coat is divided into two unequal parts by the horizontal band. The upper or larger and the lower or smaller are now divided by the same two vertical bands into three, so that there are three large and three small compartments. The central one of the larger is filled by the proboscidian sheath with the median vessel. The two larger on the sides are the lacunæ with the two posterior lobes bathing in them, and the three smaller are flat lacunæ. Each lacuna besides its own coating of epithelium and its hyaline basal layer, is surrounded by longitudinal muscular fibres. Now the middle one of the three smaller is pushed away by a mass of transverse and longitudinal muscular fibres which cause the lacuna to communicate with the two others next to it. (In my specimen, however, it opened into the left one, but this seems to be abnormal.) So we here meet again the ordinary arrangement; two lacunæ, one on each side of the proboscidian sheath, separated by a horizontal band from two smaller beneath the sheath, which in their turn are separated by a vertical transverse band. The lower or smaller embrace the stomodæum. Here and there between its folds small lacunæ remain visible. In *Cerebratulus urticans* I already had an opportunity of remarking that several of these lacunæ terminate blindly backwards, at least they disappear. The same now is the case here behind the mouth, so that only a few sections further backwards there are no

other lacunæ visible than the two above the œsophagus and on the sides of the proboscidian sheath. These gradually turn to one side a little, and come to lie in a fold of the œsophagus, which protrudes comparatively far into its lumen. Their proper lumen was filled with a coagulum that did not show any blood-corpuscles. Exactly the same coagulum here and there presented itself in little traces on the folds of the œsophagus, especially a little to the left and right of the median line ventrally, so that I am convinced that round the œsophagus the lacunar system occurs, though reduced to a minimum. The hindmost part of the œsophageal region and the rest of the body were absent.

From another specimen I could examine some sections which were probably from the hindmost part of the œsophageal region. Here the œsophagus is surrounded by lacunæ. Above the œsophagus, at the sides of the proboscidian sheath, two larger ones were present. In the lacunæ surrounding the œsophagus here and there parts of the nephridial system were distinctly visible. In the lateral angles of the lacunæ above the œsophagus a longitudinal nephridial canal was distinctly to be seen lying partly in the longitudinal muscular layer. Everywhere the lacunæ were richly coated by the epithelium that rested on a relatively massive layer of hyaline basal tissue.

In both the specimens the vessel in the proboscidian sheath again showed the remarkable difference of structure in its dorsal and ventral half.

In a third specimen, in which only the head and the foremost half of the œsophageal region were cut sagittally, I convinced myself of the presence of even very large lacunæ in this part of the œsophagus.

## 12. *Langia formosa* (Hubr.), figs. 62—64.

The vascular system corresponds to the type of that of the *Schizonemertini*.

The aperture of the proboscidian sheath is nearly terminal.

In the same slice in which this aperture lay I also saw the first trace of the lacunar space above it. The circular muscular layer is at first only present as an upper arch, which gradually grows round and closes beneath the proboscidian sheath. This now lies against the lower arch of the circular muscular layer. Here again the proboscidian sheath has not to penetrate the circular layer. The lacuna is single and horseshoe shaped, with its legs downwards. Already quite anteriorly longitudinal fibres are visible, which are everywhere numerous. The sheath leaves its position, going upwards, the lacunæ thereby taking the shape of a circle in transverse sections. This is only apparently abnormal, for we may say here that the arch of the lacunæ above the sheath is very broad—so broad that it disappears when the lower arch is already visible. This lacunar ring is only really visible in three slices, for the proboscidian sheath reaches the upper arch, and the lacuna is again horseshoe-shaped, with its legs upwards. Exactly above the lower brain-commissure the median vessel in the proboscidian sheath communicates with the lacuna. Nowhere did I see this process so distinctly as here. The vessel was swollen, filled with blood-corpuscles; the opening was so large that it seemed that the wall of the proboscidian sheath was broken there. After this the horizontal band again becomes visible, dividing the lacuna into three—two on the sides of the proboscidian sheath, which gradually embrace the posterior lobes, and the third lying beneath the sheath. This third lacuna is soon divided by three vertical bands going from the sides of the proboscidian sheath downwards. Soon, however, these three lacunæ are pushed sideways by a mass of transverse and longitudinal fibres, and whilst the horizontal band disappears communicate with the two large lacunæ on the sides of the proboscidian sheath. The posterior lobes are still visible in these latter lacunæ. The mouth of *Langia*, as it seems to me, lies further backwards than in other genera. The two lacunæ have by this time coalesced with those two in which the posterior cerebral lobes bathe, and now surround the œsophagus. As in *Cerebratulus* in all the lacunæ, except in those ventrally from the



œsophagus, the nephridial canals float. They are not attached against the longitudinal muscular layer (or this is a peculiarity of the specimen I examined?). The nephridial canals here are thicker and more distinct than I have ever seen, but have the same character as all the nephridial canals hitherto examined (of course with the exception of *Carinella*). In one of the canals I very distinctly saw cilia a little longer than the cells.

I have found only one pair of excretory ducts. They were very easily to be observed, not only lying above the nerve stems, but were even directed straight upwards, and their pores lay in the longitudinal dorsal groove or fold formed by the upwards-turned edges of the body (cf. Hubrecht, 35). About the region of the two pores the medial vessel left the proboscidian sheath, having shown again, as in all *Schizonemertea*, the different character in its upper and lower wall. Behind the pores the nephridial system extends still a little further backwards.

In the meantime the lacunæ surrounding the œsophagus have gradually become larger, and afterwards again smaller, till they pass into the two vessels situated beneath the intestine. Thus in the intestinal region we find three longitudinal vessels; they are usually united by transverse vessels, and though the diverticula are narrow I saw very distinctly a transverse vessel over each diverticulum. But these transverse vessels do not lie so closely against the diverticula as in *Valencinia*. In *Langia* they lie free amidst a gelatinous stroma with large nuclei (figs. 62—64), as do also the three longitudinal vessels. These nuclei are generally arranged round the vessel. Several of the nuclei had about them an irregular protoplasmic substance, generally showing offshoots arranged radially round the vessel. The stroma, too, presented radial arrangement, which is probably to be ascribed to local thickenings caused by the contraction of the vessel in the gelatinous tissue. Fig. 62 shows us one of the lateral (ventral) vessels cut transversely; fig. 63 the same, with an outlet of a transverse vessel, the latter, of course, cut longitudinally;



fig. 64 a portion of a transverse vessel, drawn with different focussing of a microscope.

13. *Amphiporus pulcher* (Johnst.), McInt., figs. 6, 7, 9, 38.

Of this type of *Hoplonemertea* I cannot give any summary, not having been able to examine all the details. By analogy we may, however, conclude that it is essentially the same as of *Amph. lactifloreus* (Johnst.), McInt., which will be treated subsequently.

In a head of a specimen of this species which I was able to examine, I saw very distinctly that there was only one single aperture to both the proboscidian sheath and the mouth (see also Hubrecht 35); the upper curve of the aperture is that of the proboscidian sheath, and the lower one that of the mouth. How the cephalic vascular loop (for here are no lacunæ but two vessels, which communicate anteriorly, figs. 6,7,9) is situated in relation to the proboscidian sheath I have not seen. In some slices I believe I saw the two vessels; they lay laterally (see fig. 38) and within the longitudinal muscular layer. In this area also the whole nervous system is situated. I have not observed whether the two vessels go through the cerebral ring, nor how the dorsal vessel communicates with it. But I could very well see that the dorsal vessel lies in the proboscidian sheath, but only for some twenty sections; it then leaves it. A little behind the brain I first saw very distinctly the two lateral vessels. They lie through the whole length of the body, beneath the level of the nerve-stems.

In two portions of the intestinal region I did not see transverse vessels. In a tail-piece I found them lying above each diverticulum. The mutual communication of the three longitudinal vessels is the same as in the *Schizonemertea*, above the intestine and before the anal commissure of the lateral nerves.

Of the nephridial system I may mention that Prof. Hubrecht has found in one specimen that the excretory ducts of the system lie just behind the ganglia. He had noted it down on the preparation. These ducts are very easily to be seen,

for they have very thick walls. I have examined the preparation very closely, but I did not see any more ducts. Thus, in this species, there is but one single pair of ducts, not in the posterior part but quite anteriorly. In front of the excretory ducts there is no trace of nephridial system. I have no histological facts to record.

14. *Amphiporus lactifloreus* (Johnst.), McInt., figs. 9, 10, 38—40.

The mouth and the proboscidian sheath have together only one aperture, nearly terminal and on the ventral side. This was first seen by Prof. Hubrecht, who noted it down on his preparation. I saw very distinctly in this preparation that the proboscidian sheath falls into the stomodæum; and this is, as we know, not behind but far before the ganglia. Above this stomodæum, thus also above the proboscidian sheath, goes the loop which unites the two vessels of the head (fig. 9). Of this loop we at first observe an ellipsoidal lumen, then a dumb-bell shaped one; and, finally, two lumina, being the transversally cut vessels. These two are gradually placed wider apart. Their wall consists of a very thick hyaline basal layer. They finally lie laterally to the proboscidian sheath and the œsophagus (fig. 38).

The brain respirators are very small. Their aperture is the foremost part of the whole organ. (They lay in the slice No. 31. The slices had a thickness of  $\frac{1}{50}$  mm. The specimen, in spirits, measured 17 mm. in length and 2 mm. in thickness.) The canals run backwards, lying beneath and contiguous to the vessels. A thick nerve-stem connects them with the ganglia. They soon disappear (slice No. 41).

The blood-vessels go upwards (No. 37), just before the lower brain commissure, between the two brain-masses and the proboscidian sheath; but in their former place they have left two remnants which soon disappear (slice No. 42). These two terminate thus blindly posteriorly (see fig. 9). Exactly above the lower brain commissure the vessels move beneath the proboscidian sheath, unite, and communicate with the dorsal

vessel in the proboscidian sheath (No. 47). Meanwhile, I saw all at once, on the sides of the sheath and above the ganglia (No. 42 and No. 46), a vessel cut transversally. There, then, are two branches, terminating blindly forwards (see fig. 9). The two vessels, after having communicated with the median vessel, go directly towards these little branches, coalesce, and go back to their former place between the brain-masses and the proboscidian sheath, leaving no trace of these peculiar blood-spaces (Nos. 49—51). The median vessel soon leaves the proboscidian sheath. It remains in the sheath only in five sections of  $\frac{1}{50}$  mm. In a younger specimen only three sections. The two lateral vessels remain on the inner side of the lateral nerves, but swing up and down, now being above and then beneath their level. I have twice closely examined the 800 slices, made through the whole animal, and I have nowhere seen a transverse vessel. In a tail-portion, horizontally cut, however, they were present. The communication of the three longitudinal vessels in *Amphiporus lactifloreus* I saw very distinctly. It occurred again before the anal commissure, and above the intestine.

With respect to the nephridial system, I may mention the following points. It lies, as all other organs in this species, free in the gelatinous stroma, in which I could nowhere observe nuclei. It begins in the cerebral region (slice No. 42), just there where I saw the foremost point of the strange branches of the vascular system (figs. 9 and 39). The first canal I saw lay so close to this branch that it will not surprise me if another naturalist finds there an open communication between the two systems. At all events, I have not seen it myself, though I believe I have seen that the tissues were here intimately joined. The canals showed the well-known structure. They swung very irregularly round the lateral nerves, remaining always next to them. I have found here again more than one pair of excretory ducts. These lay in the following sections.

To the Left.		To the Right.
52, 53, 54, 55 . . .		55, 56, 57
— . . .		57, 58, 59, 60
62, 63, 64 . . .		62, 63
— . . .		65, 66, 67, 68 }
— . . .		65, 66, 67, 68 }
— . . .		73, 74, 75
77, 78 . . .		—
— . . .		84, 85 }
85 . . .		85 }
— . . .		91
97, 98 . . .		—
— . . .		101

In No. 110 the nephridial system ceased, and the first genital organs became visible. This is the limit then between the œsophageal region and the intestinal. We clearly see how irregularly even the excretory ducts are arranged. Properly speaking, there are only three pairs, the other seems to be uneven. I have written in a row the numbers of the slices, in which the same duct was to be seen (running obliquely to the periphery). Two ducts on the right are twice united by an accolade. These are peculiar phenomena not hitherto observed by me in other Nemerteans. The ducts 65, &c., in the first accolade were parallel to each other (fig. 40), visible on the right side of four subsequent sections, and one beneath the nerve-trunk. The second peculiarity is this that the ducts 84 and 85 on the right had one and the same aperture through the basal membrane and the skin !

#### 15. *Amphiporus marmoratus*, Hubr., fig. 38.

The mouth and the proboscidian sheath have a common aperture. I could not, however, ascertain to which this aperture belongs, because the proboscidian sheath was widely stretched by the extruded proboscis. The cephalic loop was very distinctly visible. It ran above the common aperture, thus also above the proboscidian sheath. The two vessels then ran on the sides of the proboscidian sheath and the intestine (as in fig. 38). The brain-respirators lie beneath them, but do not touch them.



They move just before the cerebrum, a little upwards, next to the proboscidian sheath, and whilst going with this through the cerebral ring, they protrude downwards between the sheath and the brain-masses. In the specimen I examined something abnormal took place. The left vessel did not reach the ventral surface of the sheath, the right one did; it was very much enlarged, and filled with blood-corpuscles (diastole?) and communicated with the vessel in the sheath. The vessels remain where they are, they do not go upwards, because the brain-masses move sideways and diminish, and the lower commissure disappears. The vessels go downwards but remain above the level of the lateral nerves. The median vessel left the sheath after twenty-four slices (I estimate them to be one thirtieth of a mm. The body had a width of one mm.), and some ten slices behind the lateral vessels move beneath the level of the lateral nerves.

With regard to the nephridial system, it lies behind the ganglia. It consists of a very crooked canal above the lateral nerves. After twenty-five slices it disappeared, and thus it is very short. I did not see any communication with the vascular system. At the first appearance of the system on contemplating the slices from the front to the hind part, the two excretory ducts were very distinctly visible. Thus they are as much as possible in the front. Together with the whole system they are situated above the lateral nerves, but instead of running nearly horizontally towards the skin, they proceed almost vertically downwards, and so these ducts have ventral apertures.

Neither of the vascular, nor of the nephridial systems, can I mention any histological particulars.

16. *Amphiporus hastatus*, Mc.Int., figs. 8, 13,  
53, 63, 64, 70, 71.

The mouth and the proboscidian sheath have again a common, almost terminal aperture. The proboscidian sheath falls into the stomodæum just before the lower brain commissure. Brain-respirators absent.

I did not find a vascular loop in the head, nor the two vessels

which in other *Hoplonemertea* form such a loop. And yet the whole head (fifty-seven slices of  $\frac{1}{40}$  mm. in thickness) was very well preserved, judging from certain other peculiarities.

Between the stomodæum (which has three distinct layers, an inner epithelium layer, a hyaline basal layer, and a circular muscular layer) and the muscular layer of the skin (which consists here only of the circular muscular layer, outside which lie the basal membrane and the skin) we meet in the anterior sections (e. g. the tenth) with three layers. Both against the circular muscular layer of the stomodæum and against the circular muscular layer of the skin we find situated a layer of large vesicular cells, with large nuclei, and between these two gelatinous stroma occurs. The two layers of large cells are not of one row of cells; the layer against the skin had from two to three, the other from four to six rows of cells. The cells are arranged more or less radially in both layers. At the common aperture we see that the epithelium of the stomodæum passes into that of the skin, the hyaline basal layer into the basal membrane of the integument, the two circular muscular layers and the two layers of large vesicular cells into one another. (The layer of gelatinous stroma between the two latter of course ceases in front.) The more we go backwards the more in the two layers of cells do longitudinal muscular fibres become visible. In the layer next to the skin this happens through the whole thickness of it, but not in the inner layer. In the inner layer the arrangement is thus that we can distinguish an internal layer of numerous nuclei (as are figured in figs. 63 and 64 of Langia) and an external layer of longitudinal muscular fibres, which are arranged in groups. The number of the nuclei just mentioned diminishes on approaching the brain, so that this layer close to the brain obtains more the character of gelatinous stroma. Gelatinous stroma thus fills the space between the two layers of longitudinal muscular fibres, and also the area within the inner longitudinal muscular layer, in which area lie the central nervous system, proboscidian sheath, intestine, vascular system, and generative organs.

The outer layer of gelatinous stroma is relatively the

broadest in the tip of the snout, is still uninterrupted in the cerebral region, but becomes further backwards ever narrower, more so ventrally than dorsally, so that about slice 110 the two longitudinal muscular layers ventrally unite. In section 160 the same takes place on the sides and dorsally, so that further backwards *Amphiporus hastutus* is in the main not to be distinguished from any other *Hoplonemertean*.

In the layer of gelatinous stroma before the brain and between the two layers of vesicular cells are seen isolated single or groups of the same cells. These are, when isolated, round or ellipsoidal, but when in groups, like soap-bubbles, more polygonal; their size varied from fourteen to thirty micmm. Their contents are transparent, however, with a fine granulation, which apparently is protoplasm, and which sometimes, as in vegetable cells, lay round the nucleus, and sent threads to the walls of the cells, thus forming irregular star-shaped figures. I also saw cells in which the protoplasm was distinctly arranged against the inner side of the cell membrane. Then the nucleus also lay against the wall. These groups of cells diminished backwards, so that in the cerebral region still a few groups are visible, and still further backwards none occur. The more these groups disappear the more very small vessels become visible, which, occurring even in the tip of the snout, bear a highly primitive character. Sometimes, but rarely, they appear to be simple lumina in the gelatinous stroma; their wall is merely a modified hyaline gelatinous tissue, which absorbs more colouring matter than the surrounding. Sometimes, outside the hyaline basal layer, a few large nuclei are situated, exactly resembling those of the vesicular cells. Most frequently, however, these lumina are limited by some, often by a closed ring of vesicular cells (see fig. 70). Such a vessel seen in profile has the appearance of fig. 71.

I was not able to trace these vessels. They seem to pass into one another, forming a reticulum. I have illustrated it in fig. 8. A transverse section, however, through the head has a totally different appearance from one through the head of *Valencinia longirostris* (see figs. 13 and 53).



In the slices between the regions of the upper and lower brain commissures I observed in the gelatinous tissue between the proboscidian sheath and the brain-masses a larger vessel than the other. They approach each other till they come beneath the proboscidian sheath, and communicate with the dorsal vessel, which only in this single slice lay in the sheath, the four following in its circular muscular layer, and in the fifth already beneath the sheath.

Behind the lower brain commissure I saw the vessels again separated, running downwards till they lie beneath the level of the nerve-trunks.

Behind the brain we again have an œsophageal and an intestinal region.

In the œsophageal region I again observed the same small vessels in the two layers of gelatinous tissue, uniting with one another by branches traversing the inner longitudinal layer. The vessels within this layer also communicate with the three longitudinal vessels. They are all arranged in certain regions. Beneath the œsophagus transverse vessels run from the one lateral vessel to the other. From the median vessel to these transverse vessels, rarely directly to the lateral, other transverse vessels occur. But also transverse vessels, hitherto never seen, running over and above the proboscidian sheath, connecting the two lateral and passing towards the nerve-chords, are everywhere to be observed. It is very probable that between all these transverse vessels, which all resemble one another (as fig. 71), there still exist connecting vessels, so that the whole is a vascular network. This, however, is not easily to be demonstrated in transverse sections.

In the œsophageal region two longitudinal vessels are very often visible above the nerve-trunks, therefore dorsolateral. These did not always occur, so that I do not believe that there is (on each side) one uninterrupted longitudinal vessel, but fragments of it. The transverse vessels which go over the proboscidian sheath, always opened into the longitudinal vessels above the nerve-stems, where they occurred. These longitudinal vessels thus are connecting vessels between the transverse



ones. From these dorsolateral vessels I often observed delicate branches running almost straight to the periphery, above the lateral nerves. Never, however, did I succeed in finding a piercing of the basal membrane or of the skin. Do they terminate blindly? It is to be hoped that some later observer may find the excretory ducts of this nephrical system, for I do not doubt but this system of fine canals and dorsolateral vessels belongs to a nephrical system. (Compare the nephrical system of all *Hoplonemertea* in which the principal (longitudinal) canal also always lies more or less above the nerve-trunks!) I hesitated to represent the system in my illustration (fig. 8) on account of its complicated character.

In histological structure the nephrical (?) canals do not deviate from the transverse vessels of the vascular system (figs. 70, 71), even the dorsolateral, and the transversely cut connecting points occasionally visible between the transverse vessels above the proboscidian sheath, had the same structure only they were larger. They all exhibited an outer ring of large vesicular cells, round a hyaline basal layer, in which were some large granular nuclei, which were not to be distinguished from all other nuclei in the gelatinous stroma of the head or of the vesicular cells themselves. The nuclei lay in a fine granular layer. Are these nuclei blood-corpuscles and is this fine granular layer blood-coagulum, or do they both belong to the coating of the vessels? This I could not decide.

The median and the two ventrolateral vessels had between the basal layer and the ring of vesicular cells a layer of circular muscular fibres.

In the intestinal region the transverse vessels run over only a few of the diverticula. In the tail, however, they occur more frequently, yet here and there skipping a diverticulum.

The lateral vessels always lie beneath the nerve-stems, not beneath the intestine.

#### 17. *Drepanophorus rubrostriatus*, Hubr., fig. 7, 42.

The vascular system consists of a cephalic loop, running above the proboscidian sheath. (Proboscidian sheath and

mouth have each their own aperture, nearly terminal.) The passage through the cerebral ring and the communication with the median vessel, which only in the œsophageal region lies in the sheath, are similar to what occurs in all *Hoplonemertea* with cephalic loops. In the œsophageal region no transverse vessels occur, in the intestinal region, however, they do. The communication in the tail is normal.

The nephridial system lies, in the œsophageal region, entirely above the nerve-trunks, and always has numerous windings, so that nearly always more than one transversely cut canal is seen in sections. If we bear the fact in mind that a winding canal must always show three, five, or seven sections, and if we then see in a slice four sections of canals, we must conclude that at least one of these canals is a branch. As I often observed an even number, so I suggest that there are many branches, as I have represented in fig. 7. The excretory ducts lie in the midst of the œsophageal region, above the nerve-trunks, and curve downwards, having ventral apertures. Fig. 42 exhibits a section through the œsophageal region of *Drepanophorus*.

From the proboscidian sheath lateral sacs proceed between the intestine and the nerve-trunks, arranged in pairs and ranging from the ganglia to the end of the proboscidian sheath. McIntosh was the first (24) who observed this peculiarity of the sheath of *Drepanophorus*. He saw on sagittal sections openings through the lateral walls of the proboscidian sheath, and represents them, but without further tracing what these openings are. He, however, concluded that these openings (stomata) form the connection between the vascular system and the proboscidian sheath. Hubrecht (35) recognised the true nature of these organs, calling them "membranaceous sacs." I have exerted myself to trace, on transverse as well as on horizontal sections, these peculiar spaces. They are only blindly terminating tubes, sometimes very much dilated and at their extremities sac-shaped. They generally run with a downward curve. Only once I found a communicating branch (longitudinal) between two of these sacs. Their open-

ing into the sheath was sometimes wide; most frequently, however, so closely contracted that only a high power enabled me to see any aperture.

It is not my purpose to give an explanation of these sacs or to trace their histological structure, but they are not connected with the vascular system.

The medial blood-vessel in the proboscidian sheath is attached with a very small base, so that it is almost totally bathed by the fluid of the sheath. But I did not observe that its upper wall had a different structure from that of the lower one. The epithelium of the sheath covers the vessel. The hyaline basal layer of the proboscidian sheath passes into that of the vessel, and just beneath the vessel a few longitudinal muscular fibres are situated. The median vessel, when beneath the proboscidian sheath, and the two lateral vessels, have outside the hyaline basal layer some circular muscular fibres. Within the hyaline basal layer the common epithelium is again present. The nephridial canals exhibit the same structure as in all other species.

#### 18. *Drepanophorus serraticollis*, Hubr., fig. 65.

The mouth and the proboscidian sheath have each their own aperture. I could see the cephalic loop distinctly above the proboscidian sheath. Transverse vessels were present in a tailpiece at the tip of the tail, where the three longitudinal vessels pass into one another. The transverse vessels cut transversely resemble those of *Cerebratulus marginatus* (fig. 65).

#### 19. *Tetrastemma candidum* (O. F. M.), Oerst., figs. 6, 38.

I did not observe that the cephalic loop went over the proboscidian sheath. The preparation was not sufficiently preserved to enable me to see it. I clearly saw the two vessels of the loop (fig. 38). In the usual way they protrude between the brain and the proboscidian sheath, descend along the sides of the sheath, and communicate just below the proboscidian

sheath and behind the lower brain commissure with one another and with the median vessel, which in *Tetrastemma* never lies in the proboscidian sheath. The two lateral vessels descend further between the lateral nerves and the œsophagus, and lie beneath the level of the nerve-stems, so that they are ventral, the nerve-stems already being situated ventrally. The preparation was too imperfect to allow of the detection of transverse vessels. Perhaps they exist.

## 20. *Nemertes gracilis*, Johnst.

The specimen was cut sagittally, and about 23 mm. in length.

In the hindmost part I distinctly saw transverse vessels running over the diverticula. They have no circular muscular fibres round the basal layer.

The nephridial system is of unusual length, for in a specimen about 23 mm. long and 1 mm. wide I saw behind the ganglia one nephridial canal, and about 8 mm. from the tip of the snout two canals. Concerning their histological particulars I can make no definite statements.

## 21. *Malacobdella grossa* (O. F. M.), Blainv., fig. 3.

I am unable to correct Von Kennel's description, either of the vascular or of the nephridial system. I will merely give some additional observations.

The cephalic loop runs over the proboscidian sheath, as in all other Nemertea. Not only from the two lateral vessels, but also from the cephalic loop numerous branches arise. In my specimen the median vessel had none.

I could observe cilia, both in the two chief canals and in the excretory ducts of the nephridial system. The chief canals anteriorly lie above the nerve-trunks, then backwards; they assume a more lateral position, and finally send the excretory ducts with a little curve round above the nerve-stems; they thus communicate ventrally with the exterior.



## SUMMARY.

We have seen that there are three types of vascular system in the Nemertea. Though the families of the Valenci-niidæ and the Poliidæ belong to the Palæonemertea, they, with respect to their vascular and nephridial system, already approach the Schizonemertea. To avoid confusion, I will here employ the expressions, "Palæo-type," "Schizo-type," and "Hoplo-type."

In the Palæo-type we have two longitudinal blood-spaces, which communicate forwards in the head above the proboscidian sheath, are lacunar in the head and the œsophageal region. They have in the œsophageal region a tendency to enlarge their surface, but are true vessels in the intestinal region, and communicate in the tail above the intestine.

In the head also, lacunar communications may occur beneath the proboscidian sheath. In the œsophageal region the surface is enlarged, owing either to the fact that the lacunæ are large (Cephalotrix), or that portions are constantly being detached, which, however, remain in open connection with the principal lacunæ (Carinella), or that along the whole œsophageal region the lacunæ have divided into two stems, which only in the foremost part permanently communicate (Carinoma).

The vessels in the tail of Carinella open directly into one another, thus forming a loop above the intestine. In Carinoma lacunar spaces communicate above the proctodæum, representing rudimentary transverse vessels.

Moreover, in some forms of the Palæo-type (Carinella, second form of Carinoma) two other vessels occur in the œsophageal region and in the proboscidian sheath. Their connection with the vascular system could only be demonstrated with certainty in exceptional cases.

In the Schizo-type we find: in the head, lacunar spaces which communicate both above and beneath the proboscidian sheath; in the œsophageal region also, lacunar spaces which coalesce round the œsophagus on the ventral side. Two lacunæ on the sides of the proboscidian sheath are more permanently

distinct and separate from the rest. In the remaining portion of the body, three longitudinal vessels, connected by transverse vessels, are present. The communication in the tail lies above the intestine.

In the œsophageal region we find only one single vessel in the proboscidian sheath. Anteriorly, this is connected with the lacunar communication beneath the proboscidian sheath, piercing its lower wall. Posteriorly, it also pierces the lower wall of the sheath, and is continued into the median vessel lying under the proboscidian sheath.

In the lower forms (Valenciniidæ) the two lacunæ on the sides of the proboscidian sheath continue further backwards. The transverse vessels, which otherwise only connect the three longitudinal vessels, in that case also enter into communication with these lacunæ.

The third type, the Hoplo-type, is especially characterised by the absence of lacunar spaces. Here there is a closed vascular system. Here we find (excl. *Amphiporus hastatus*, McInt.) in the head two vessels which communicate in front, forming a vascular loop, above the proboscidian sheath. These vessels also communicate within the cerebral ring, but now beneath it. From this point down to the tail three longitudinal vessels occur, of which the median vessel in the œsophageal region often lies partly in the proboscidian sheath. In the intestinal region generally the three longitudinal vessels are united by transverse vessels. The communication in the tail lies above the intestine.

The cephalic loop may form branches (fig. 3, *Malacobdella*). The portion of the median vessel which lies in the proboscidian sheath, in this type gradually becomes shorter and shorter. There are even forms in which it no more enters the sheath, but remains beneath it along its whole length. (*Nemertes*, *Tetrastemma*, *Malacobdella*.) In the intestinal region, along the whole length, or only in the posterior portion, transverse vessels occur. In some cases, branches arise from the longitudinal vessels (more especially from the lateral ones) during sexual maturity (fig. 3, *Malacobdella*).

In the posterior sucker of *Malacobdella* numerous vascular branches are developed.

In all Nemertea the foremost communication of the vascular spaces occurs above the proboscidian sheath, the hindmost above the intestine. In all Nemertea the blood-spaces are everywhere coated internally with a layer of epithelium, then a layer of hyaline basal tissue follows always. Outside this basal layer there may lie either large vesicular cells (figs. 70, 71), or protoplasmatic cells with large nuclei (figs. 62—65), or circular muscular fibres are formed by these cells (figs. 66), or, but more rarely, longitudinal fibres are present in addition (figs. 74, 75).

With regard to the nephridia in *Carinella*, a portion of the lateral vessels is changed into such an apparatus. This apparatus here is distinctly a portion of the blood-space, separated from it, just as in the œsophageal region other portions detach themselves; it communicates both directly and indirectly with the vascular system. Indirectly, because a portion of the walls of the blood-vessel changes into a gland, the function of which appears to be to convey the superfluous matter from the blood-fluid towards a reservoir, the portion separated from the blood-vessel. This has two open communications with the blood-vessel. Thus, the separation is, as it were, still imperfect, and the points of communication appear to diverge from one another with the growth of the animal. The secretions of the nephridial glands must be removed, therefore an excretory duct is developed on each reservoir. The two excretory ducts lie nearly on the same transverse level, so that, if the animal were a segmented one, they would be found in the same segment. They are generally contracted by the basal-membrane and the skin, so that no sea-water can enter the reservoir but by an inner impulse caused by the muscular walls of the reservoir the ducts may open. I suppose that the removal of the secretions happens periodically. Thus the nephridia of *Carinella*, the lowest type of Nemerteans, in which up to this time a nephridium has been found, is highly primitive.



Of higher development is the nephridial system of *Carinoma*. The function of removing the waste products is here transferred to the canals of the system itself. Here we no more find a nephridial gland. The canals, however, are coated with an epithelium, consisting of pure glandular cells. The removal of the secretion outwards would seem not to happen periodically but permanently, as each cell is provided with a long cilium directed outwards. The system, though changed so much that it cannot possibly be confounded with the vascular system, in *Carinoma*, however, still shows its primitive relation to it. There are three open connections on each side, and the whole lower arch of the blood-vessel between the first and the second communication is changed into a tissue which closely resembles that of which the nephridial canal consists. Thus, we have here also a portion of the nephridium, which is, as it were, separated from the blood-vessel, of which the traces are still present! The two excretory ducts here lie also in the same transverse plane.

In the Schizo-type the nephridium lies wholly in the lacunar spaces of the œsophageal region. In some species it extends still a little further into the intestinal region. The whole system is generally situated against the inner side of the inner longitudinal muscular coat. There are, however, types where it seems to float in the lacunæ (*Langia*). In most species I could not distinguish the exact arrangement. In *Valencinia*, however, the form is that of a ladder, and on the level of each step there is an excretory duct. Thus there are two longitudinal canals and numerous transverse ones. They are, however, all of the same size. The whole indicates a segmental arrangement. The same is found in *Polia* and *Lineus*. In these two genera I could not, however, trace the form of the system, but it seems to me that here too the canals are all of the same size. In *Cerebratulus* and *Langia*, however, a thicker longitudinal canal is distinctly seen, and several thinner ones. Here I could not find more than one single pair of excretory ducts. Thus, the lower the types the



more numerous are the paired ducts; the higher the types the fewer, till they are reduced to one pair.

The nephridial system of the *Hoplonemertea* also shows several degrees of complexity. It consists of numerous small canals, which are connected with a longitudinal canal on each side. These send their excretory ducts outwards. The excretory ducts are either two in number (*Drepanophorus*, *Nemertes*, *Malacobdella*, *Amphiporus pulcher*, &c.) or more [*Amphiporus lactifloreus* (and *hastatus*?)]. Where two occur these may be quite anteriorly situated (*Amphiporus pulcher*), in the middle (*Drepanophorus rubro-striatus*), or posteriorly (*Malacobdella*).

Thus the nephridial system of all the *Nemertea* consists of one or more canals, directly communicating or not with the vascular system, provided or not with cilia, and communicating with the exterior by means of excretory ducts. These excretory ducts all lie above the nerve-trunks.

I now wish for a moment to summarise the very provisional hypothesis, which I have ventured to make respecting the physiological function of the two proboscidian sheath-vessels in the *Palæo*-type of the median vessel, lying in the proboscidian sheath in the two other types, and of the membranaceous sacs of *Drepanophorus*.

McIntosh was the first who, both in the *Schizo*-type and the *Palæo*-type, mentioned a vessel which lay in the proboscidian sheath. Dewoletzky was the first to mention this median vessel in the sheath in a representation of the *Hoplo*-type (*Drepanophorus*). In *Lineus marinus*, in the foremost part of the œsophageal region, McIntosh found one median vessel lying in the sheath, and described in *Carinoma Armandi* two vessels in the sheath. In his description of the latter he says: "The physiological signification of these two vessels is clear since the discovery of a regular series of vessels which communicate with the proboscidian sheath."

This passage can hardly be said to clearly explain what physiological significance McIntosh ascribes to this arrangement, and as far as it applies to the existence of an open com-

munication between the vascular system and the proboscidian sheath, I must distinctly negative it as far as my own experience goes. I therefore wish to suggest another hypothesis, viz. that the two blindly terminating vessels in the proboscidian sheath of the Palæo-type, as well as that portion of the median vessel which lies in the proboscidian sheath in the Schizo- and Hoplo-type, and "the membranaceous sacs" (Hubrecht) in *Drepanophorus*, are intended for purposes of respiration, nutrition, and excretion of the fluid contained in the proboscidian sheath.

It is superfluous here to resume all the reasons which have led me to this supposition. I beg to refer the reader to what has been stated above, where this subject was more extensively alluded to.

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- For nomenclature Nos. 18 and 35 have served me.

## EXPLANATION OF PLATES I, II, and III,

Illustrating Mr. A. C. Oudemans's Memoir on "The Circulatory and Nephridial Apparatus of the Nemertea."

In Plates I and II the blood-spaces are marked red, the nephridia blue. The short lines accompanying the figures in Plate I show the levels at which the transverse sections have been obtained which are figured in Plate II. The numbers placed on these lines correspond to the numbering of the figures in Plate II.

Plate II only contains figures of transverse sections. All that is grey belongs to the nerve system. *I.* Intestine, and *Ps.* Proboscidian sheath.

The figures in Plate III are all drawn by means of the camera lucida, Figs. 55—61 with a Zeiss, obj. E, oc. 2, and Figs. 62—75 with a Siebert, obj. imm. No. 7, Periscopic ocular.



## PLATE I.

FIG. 1.—Diagram of the vascular system in the head, the œsophageal region, and the intestinal region of *Cephalotrix linearis* (Rathke), Oerst.

FIG. 2.—Diagram of the vascular system (1st form) in the head and œsophageal region of *Carinella annulata* (Mont.), McInt.

FIG. 3.—Diagram of the vascular system and the nephridial system of *Malacobdella grossa* (O. F. M.), Blainv.

FIG. 4.—Diagram of the vascular system (2nd form) and the nephridial system in the head and the œsophageal region of *Carinella annulata* (Mont.), McInt.

FIG. 5.—Diagram of the vascular system and the nephridial system in the head and the œsophageal region of *Carinoma Armandi* (McInt.), Oud.

FIGS. 6 and 10.—Diagram of the vascular system of *Tetrastemma candidum* (O. F. M.), Oerst.

FIGS. 7 and 10.—Diagram of the vascular system and the nephridial system of *Drepanophorus rubrostriatus*, Hubr. The portion of the median vessel drawn in the figure between two white interruptions lies in the proboscidian sheath.

FIGS. 8 and 10.—Diagram of the vascular system of *Amphiporus hastatus*, McInt.

FIGS. 9 and 10.—Diagram of the vascular system and the nephridial system of *Amphiporus lactifloreus* (Johnst.), McInt. The portion of the median vessel drawn in the figure between two white interruptions lies in the proboscidian sheath.

FIG. 10.—See Figs. 6, 7, 8, and 9.

FIGS. 11 and 12.—Diagram of the vascular system and the nephridial system of *Polia curta*, Hubr. The portion of the median vessel drawn in the figure between two white interruptions lies in the proboscidian sheath.

FIGS. 13, 14, 15, and 16.—Diagram of the vascular system and the nephridial system of *Valencinia longirostris*, Quatr. The portion of the median vessel drawn in the figure between two white interruptions lies in the proboscidian sheath. Fig. 14 immediately unites with Fig. 13.

FIGS. 17 and 18.—Diagram of the vascular and the nephridial systems of *Lineus sanguineus* (Rathke), McInt. The portion of the median vessel drawn in the figure between two white interruptions lies in the proboscidian sheath.

## PLATE II.

## Transverse Sections.

FIGS. 19—21.—*Cephalotrix linearis* (Rathke), Oerst. See Fig. 1.

FIG. 19.—Through the præcerebral portion.

FIG. 20.—Through the cerebral portion (cerebral ring).

FIG. 21.—Through the œsophageal region.

Figs. 22—27.—*Carinella annulata* (Mont.), McInt. See Figs. 2 and 4.

FIG. 22.—Through the intestinal region.

FIG. 23.—Through the œsophageal region to the left, curving downwards, and to the right upwards, thus becoming partially lacunar.

FIG. 24.—Ditto, with two vessels in the sheath. The lateral vessels, each with an arch upwards, partially lacunar.

FIG. 25.—Through the nephridial region. The left half of the figure shows a blood-vessel with the spongy nephridial gland lying in it, and a nephridial canal. The right half shows the same as the left one, but, in addition, the foremost open communication between blood-vessel and nephridial canal.

FIG. 26.—Ditto. The left half shows the blood-vessel and the hindmost open communication between this and the nephridial canal. The right half shows the blood-vessel with the spongy nephridial gland lying in it, and a communication of the nephridial canal with this gland.

FIG. 27.—Ditto. The two only excretory ducts of the nephridial system are situated in this section.

Figs. 28—37.—*Carinoma Armandi* (McInt.), Oud. See Fig. 5.

FIG. 28.—Through the tip of the snout. Point of junction of the four large lacunæ.

FIG. 29.—Through the præcerebral region. Four large cephalic lacunæ are visible, two on each side of the proboscidian sheath.

FIG. 30.—Through the cerebral portion. The four lacunæ have coalesced to form two, and with the proboscidian sheath protrude through the cerebral ring.

FIG. 31.—Through the postcerebral region. The mouth lies in this section. Mutual connection between the six vessels: two lateral vessels, two supra-proboscidian sheath-vessels, and two vessels lying in the sheath.

FIG. 32.—Through the œsophageal region. The six longitudinal vessels are visible.

FIG. 33.—Through the nephridial region. The vessels above and in the sheath have disappeared, terminating blindly. The two blood-vessels and the nephridial canals are visible.

FIG. 34.—Ditto. The two only excretory ducts are visible in this section. The dotted line in Fig. 5 shows the direction of the imaginary sections represented in our Fig. 34.

FIG. 35.—Ditto. On each side a blood-vessel and two nephridial canals.

FIG. 36.—Ditto. The two nephridial canals coalesce.

FIG. 37.—Ditto. Hindmost communication between blood-vessel and nephridium.

FIG. 38.—Through the præcerebral region of *Tetrastemma candidum* (O. F. M.), Oerst. See Fig. 6.

Figs. 39 and 40.—*Amphiporus lactifloreus* (Johnst.), McInt. See Fig. 9.

FIG. 39.—Through the præcerebral region.

FIG. 40.—Through the œsophageal region. Excretory ducts of the nephridial system, both above and below the nerve-trunks.

FIG. 41.—Through the intestinal region of *Hoplonemertea* (excl. *Mala-cobdella*), *Schizonemertea*, *Valenciniidæ*, and *Poliidæ*. See Figs. 10, 12, 16, and 18.

FIG. 42.—Through the œsophageal region of *Drepanophorus rubro-striatus*, Hubr., with two membranaceous sacs of the proboscidian sheath, and the two only excretory ducts of the nephridial system.

Figs. 43—51.—*Polia curta*, Hubr. See Fig. 11.

FIG. 43.—Through the præcerebral region. The foremost lacunæ do not communicate with one another.

FIG. 44.—Through the cerebral region. Communication between the cephalic lacunæ above the proboscidian sheath.

FIG. 45.—Ditto. The lacunæ on the sides of the proboscidian sheath at first coalesce beneath the sheath and then divide into three parts, one of which lies beneath the sheath.

FIG. 46.—Ditto. Communication between the cephalic lacunæ and the median vessel in the proboscidian sheath.

FIG. 47.—Ditto. Communication of all the lacunæ, which now spread over the brain lobes.

FIG. 48.—Through the postcerebral region. The posterior lobes bathe in the lacunæ.

FIG. 49.—Ditto. The forward projecting part of the stomodæum bathes in the lacunæ, partly lying above the posterior lobes, which are still visible.

FIG. 50.—Ditto. The mouth lies in the section. Two lacunæ, one on each side.

FIG. 51.—Through the œsophageal region. The lacunæ surround the œsophagus, except on its dorsal surface. The nephridial system lies in the lacuna against its outer border. Two of the excretory ducts are severed by the section.

Figs. 52, 53.—*Valencinia longirostris*, Quatr. See Fig. 14.

FIG. 52.—Through the foremost part of the intestine. The œsophageal lacunæ are continued into the two lateral (ventral) vessels, and the two lacunæ on the sides of the proboscidian sheath. (The median vessel here lies beneath the sheath.) The five vessels are united by transverse vessels.

FIG. 53.—Through the præcerebral region, in front of the opening of the proboscidian sheath. Numerous cephalic lacunæ.

FIG. 54.—Through the cerebral region of *Lineus sanguineus* (Rathke), McInt. (cerebral ring). The abnormal method of communication between the cephalic lacunæ and the median vessel. See Fig. 17.

## PLATE III.

FIG. 55.—The median vessel leaves the proboscidian sheath in the œsophageal region: drawn from a preparation of *Valencinia longirostris*, Quatr.

FIG. 56.—Foremost open communication of the nephridial system with the blood-vessel in *Carinoma Armandi* (McInt.), Oud. The true nephridial canal arises from the tissue of the wall of the vessel, which in the neighbourhood of the opening is of totally different structure from the rest.

FIG. 57.—Second open communication of the nephridial system with the blood-vessel in *Carinoma Armandi* (McInt.), Oud.

FIGS. 58, 59, 60, and 61.—A series of four transverse sections through *Carinoma Armandi* (McInt.), Oud., to justify the sketch No. 31.

FIG. 62.—Transverse section through one of the lateral vessels of *Langia formosa*, Hubr.

FIG. 63.—Transverse section through one of the lateral vessels of *Langia formosa*, Hubr., with a longitudinally-cut transverse vessel.

FIG. 64.—A transverse vessel seen lengthways in a transverse section of *Langia formosa*, Hubr.

FIG. 65.—Transverse section through a transverse vessel of *Cerebratulus marginatus*, Ren.

FIG. 66.—Transverse section through one of the lateral vessels of *Cerebratulus hepaticus*, Hubr.

FIG. 67.—Longitudinal section (vertical) through the præcerebral region (before the opening of the proboscidian sheath) of *Valencinia longirostris*, Quatr. An upper and a lower lacuna are visible in this section. Compare Fig. 53.

FIG. 68.—Transverse section through the foremost part of the median vessel, lying in the proboscidian sheath of *Polia curta*, Hubr.

FIG. 69.—Transverse section through the median vessel, lying in the proboscidian sheath of *Drepanophorus rubrostriatus*, Hubr.

FIG. 70.—A small vessel in the gelatinous tissue of *Amphiporus hastatus*, McInt., transversely cut.

FIG. 71.—Ditto, as seen lying in a transverse section.

FIG. 72.—The supra-proboscidian-sheath-vessel from the right side in *Carinoma Armandi* (McInt.), Oud., transversely divided into two.

FIG. 73.—The same, normal.

FIG. 74.—The lateral vessel of *Carinoma Armandi* (McInt.), Oud. Partly obliquely severed. An inner epithelium-layer, a hyaline basal-layer, a layer of protoplasmic cells passing into fibres which run round the vessel, and a layer of the same kind of cells which run along the vessel are distinctly visible.

FIG. 75.—The lateral vessel of *Carinoma Armandi* (McInt.), Oud., transverse section.



The Later Stages in the Development of Balanoglossus Kowalevskii, with a Suggestion as to the Affinities of the Enteropneusta.<sup>1</sup>

By

**William Bateson, B.A.,**

Scholar of St. John's College, Cambridge.

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With Plates IV, V, VI, VII, VIII, and IX.

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IN the 'Quart. Journ. Micr. Sci.' for April, 1884, I described the early stages in the development of a species of Balanoglossus, common on the shores of the Chesapeake Bay. I am led from various reasons, which I hope to detail when an opportunity occurs for discussing the classification of the Enteropneusta, to regard this species as identical with that described by Alex. Agassiz, and called by him B. Kowalevskii.

I was again enabled, during the summer of 1884, by the great kindness of my friend Dr. W. K. Brooks, to pursue my investigations into the morphology of the Enteropneusta. My warmest thanks are due to Dr. Brooks for once more affording me the hospitalities of the Chesapeake Zoological Laboratory, which was this year situated at Beaufort, North Carolina. While there I collected a number of specimens of a large undescribed species of Balanoglossus resembling B. salmoneus (Giard). This species, a description of which

<sup>1</sup> A note on the subject-matter of this paper appeared in the 'Proc. Roy. Soc.,' No. 235, 1885.

will I hope shortly appear, I propose to call *B. Brooksii*. My attempts at rearing this species from the egg were unsuccessful, and I was prevented by illness from making any additional observations on its development.

On leaving Beaufort, N. C., I returned to Hampton, Virginia, in the beginning of September, in the hope of finding the later stages in the development of *B. Kowalevskii*, and was fortunate enough to procure a complete series of larvæ from Stage H to individuals possessing ten gill-slits, in which condition the generative organs are first present. It is intended in this paper to give a general account of these stages, together with the histology of the animal, until two pairs of gill-slits are developed (fig. 1). From this point the further histological differentiation of the various organs will be described under separate headings.

With this account of the organogeny of *B. Kowalevskii* will be given, as far as possible, a comparative description of the same parts in all the species which I have hitherto examined.

**External Changes.**—The larva of *B. Kowalevskii* was described (*loc. cit.*) as leaving the egg in an elliptical form, divided by two transverse constrictions into three segments. The surface of the body was ciliated, a special tuft of long cilia being developed at the anterior end, while the posterior region was surrounded by a transverse band of long cilia.

From further observations it seems probable that this period (Stage D) assigned as the time of hatching is too early; for embryos kept in aquaria do not break the membranous shell before Stage G is reached. Probably, therefore, the larvæ found swimming in Stage D had escaped owing to an artificial rupture of the shell during the process by which they were found, an account of which is given in an appendix.

The formation of the mouth as a ventral pore in the anterior groove was described (No. 3, fig. 41). It opens directly into the archenteron, which was previously a closed sac, from which five mesoblastic pouches had been given off, forming the anterior, middle, and posterior body cavities respectively.

The external relations of the parts then become changed until finally the larva has the shape shown in No. 3, figs. 16 and 17. In this stage the proboscis is conical and the middle segment much shortened. In the anterior dorso-lateral region of the third segment are the openings of the first pair of gill-slits, which are simple circular pores leading into the archenteron.

The larva is still opaque, and pale yellowish-brown in colour. In this condition it remains for about ten days, at the end of which time the second pair of gill-slits is formed. The body has become partly transparent, especially in the region of the proboscis, through the walls of which muscle-fibres are visible. Other external changes which occur at this period are the loss of the anterior tuft of cilia and the gradual disappearance of the posterior ciliated ring. At the commencement of this period the larvæ are to be found in Stage G at a depth of about six to eight inches in the sand, but towards its close they work their way into the higher strata of mud, and do not again go down again until the adult condition is reached.

As the cilia disappear a peculiar organ is formed as a small papilla, bearing long cilia and mucous glands, situated at the central part of the posterior surface (fig. 1, *sk.*). This organ serves as a sucker, by which the animal can attach itself to foreign bodies sufficiently firmly to prevent itself being washed off by a stream of water from a pipette. The anterior surface of the proboscis is also slightly suctorial, and by thus fixing itself posteriorly and extending the proboscis it is able to creep slowly about, somewhat in the manner of a leech. The appearance of this organ bears some resemblance to the terminal sucker described by Graaf as occurring in certain Rhabdocœles. It subsequently attains a considerable size, and is traversed by several wrinkles (figs. 3 and 4, *sk.*). This organ afterwards entirely disappears, but as to its mode of disappearance I have no certain observations. It would appear to occur very suddenly at the stage when the animal possesses seven to eight gill-slits. I have found animals with eight gill-slits which possess this sucker, and also animals of apparently the

same age without it; hence it may be inferred that it undergoes a rapid atrophy at this point.

Similar suckers<sup>1</sup> occur as larval organs in Tunicata, Ganoids, and Amphibia.

With regard to the meaning of the sucker, considering the time of life at which it appears, it is probably not ancestral in origin; as the animal is already, from Stage G onwards, a distinct *Balanoglossus* in all its characters. It is more reasonable to conjecture that it is of purely developmental importance, and indeed its use to a larva of this kind is sufficiently obvious; for the creatures inhabit shallow pools on the sand-flats, being just buried in the mud, from which position they would be in danger of being washed away by the incoming tide and so be dried up by the great heat of the sun at low tide. On attaining a larger size the body can be, and always is, coiled round a spindle of sand and thus is kept in position, hence the sucker is no more required. In connection with this sucker I observed that nearly all the animals found in these pools were such as are provided with similar means of fixing themselves, which power is probably essential to life in such a habitat. An account of the histology of this sucker will be given subsequently.

During the period which elapses between the appearance of the first and second pair of gill-slits the body gradually acquires, as was mentioned above, a considerable degree of transparency. Owing to this fact several points of internal structure may be observed. This is especially marked in the case of the alimentary canal, which can now be clearly perceived to consist of three regions—an anterior branchial tract, a middle digestive portion, and an intestinal section posteriorly. The digestive section may be at once recognised by the bright yellow-brown colour of the secretion which it contains. This fluid is evacuated after a time when the animal is irritated, but no experiments were made to determine its physiological properties.

<sup>1</sup> Balfour was of opinion that in these forms they might be an ancestral feature (Balfour, 'Comp. Emb.,' vol. ii, "Tunicata").



The partial transparency of the body wall permits also an indistinct view of the curious supporting rod of hypoblast which projects into the proboscis cavity. For reasons given later in this paper I propose to speak of this structure as the notochord (*Nch.*). The general appearance of the animal at the time when the second gill-slit appears, is shown in fig. 1. The animal is drawn as seen from the actual left side and displays the increased flexion of the body on its ventral surface.

The second gill-slit is shown as a small circular pore.

It will also be observed that that part of the body which lay between the two grooves constituting the middle segment of the body has now assumed an altered shape. At Stage H is found little more than a circular ridge on the body separating the proboscis from the trunk, while in fig. 1 (two gill-slits) it forms a kind of phlange enveloping the base of the proboscis. This change in shape is due to the operation of several causes, which are of great importance in interpreting the processes by which the final form of the adult is reached.

In the first place, after the formation of the mouth as a pore on the ventral surface, the constriction by which the proboscis is segmented off becomes deeper and deeper, until at last it is only attached by the exceedingly slender stalk shown in figs. 2 and 3. As a consequence of this process coupled with a forward growth of the ventral lip of the collar, the mouth comes to be directed anteriorly instead of ventrally (cp. figs. 7, 46 and 57). By this process the anterior phlange of the collar acquires the relation shown in fig. 1, et seq. In addition to these changes a most important structure is first formed at this time, namely, the cavity, which from the relations which it afterwards possesses I shall speak of as the atrial cavity.

In the later conditions of Stage H the body is perceptibly wider in the region of the body immediately anterior to the gill-slits than it is behind them. This increase in width, which is still very slightly marked, is due to a circular thickening which passes all round the animal, being most developed at the sides. By the time of the appearance of the second pair of

gill-slits this thickening has considerably increased, and in the contracted condition of the body is a very marked structure (fig. 2, *op.*). As development proceeds, this thickening increases, and at the same time grows backwards in the lateral regions until (five gill-slits) it has covered half the first gill-slit. The degree of contraction of the body of course alters its relations, but in the extended condition in adult specimens its posterior margin is about on a level with the fourth gill-slit. As then this structure is a process of the body wall which forms an opercular fold over the foremost gills, it appears reasonable to institute a comparison between it and the atrial walls of *Amphioxus*, &c. It will therefore be alluded to as the operculum, and the cavity between it and the body wall as the atrial cavity.

As previously described, the first gill-slit on its appearance is a simple circular pore. In this condition it remains for some days, but gradually, on about the tenth day, its form changes owing to the growth of a process from the dorsal margin of the pore, which renders the aperture somewhat kidney-shaped (fig. 1). Whilst this process is continuing the second gill-slit appears as another circular pore, similar to the original aperture of the first gill-slit. I was unable to discover any priority in the appearance of the gill-slit of either side in particular, but incline to believing that they appear synchronously on the two sides of the body, as previously mentioned.

After the appearance of the first gill-slit a definite series of changes is undergone, and these form a definite period in the history of the development of the animal, which may be considered as closing with the formation of the second pair of gill-slits.

At this point it may be well to recapitulate these changes. The embryonic life terminates with hatching, and the free larva with one pair of gill-slits escapes, moving about in the mud by means of cilia.

Before the second pair of gill-slits appear, it has undergone the following changes :

- (1) Disappearance of ciliated band and apical tuft.
- (2) Body walls have become semi-transparent.
- (3) Animal has changed its habitat, creeping into the upper layer of mud.
- (4) A fixing organ has formed as a ventral posterior sucker.
- (5) Owing to growth of collar-fold, and constriction of proboscis-stalk, the mouth comes to be directed forwards.
- (6) Differentiation has occurred in the hypoblast cells, marking out the alimentary canal into three regions, viz. branchial, digestive, and intestinal.
- (7) Notochord is distinctly visible.
- (8) Anal perforation present.
- (9) Second pair of gill-slits arise.
- (10) Opercular fold forms, as a circular thickening.

From this point onwards the principal changes in external features consist chiefly in an increase in size, and in continual progress towards transparency. This latter is so marked a feature that when three pairs of gill-slits are formed the walls of the body behind the collar, which were originally opaque, become perfectly clear and glassy, so that the internal structures are quite distinguishable. The walls of the proboscis and of the collar never entirely lose their primitive opacity. An attempt is made in figs. 1, 2, and 3 to show this gradual transition. It is presumably due to the consumption of the food particles which in the earlier condition were distributed almost uniformly among the cells of the body. This great transparency is not usual among forms that do not lead a free-swimming existence, and is possibly, so to speak, accidental, and correlated to the rapid growth which now occurs. Numerous glandular patches and spots are to be seen in the skin. They are developed chiefly on the proboscis, collar, and sucker, those on the latter being refractive and differing somewhat in appearance from the rest.

The increase in size seems to be rapid, but as to the length of time that is taken in passing through subsequent stages I have no record, as the specimens were caught from time to time, and not reared in aquaria.



As the body grows, the number of gill-slits increases. They are always added in pairs behind the last formed. The newest has a circular orifice, while the growth of the "valves" (fig. 4) from the dorsal margins of the anterior ones continues to modify their shape. From being circular they then become, first, kidney-shaped, then horseshoe-shaped, and next, by a diminution in width from before backwards; together with a great elongation dorso-ventrally, their openings are made U-shaped. When this condition is attained, the "valve" continues to grow downwards, its free end lying inside the pharyngeal cavity, as will be described when the histology of the gills is treated of. Frequently, in contracted specimens, these valves are washed outwards through the gill-slit, and hang freely out in the water. This condition often occurs during life. The gill apertures are from the first strongly ciliated. The cilia move in a constant direction, driving a current dorsalwards on the anterior line of the U, then down the anterior margin of the "valve" and up the posterior, and finally ventralwards on the hinder edge of the gill-slit. The currents have the same course before the formation of the "valve," viz. on looking at a circular gill-slit of the left side, if the animal's head is directed to the observer's left, the course will be round the aperture in the direction of the hands of a watch. By this current the water which passes in at the mouth is carried out of the pharynx; probably, therefore, the motion of the cilia is in a sort of spiral converging outwardly, and not circular as it appears to be on looking down upon a gill-slit.

From the fact that the number of gill-slits varies with the length of the animal, together with the constant presence in the posterior branchial region of a regularly arranged series of gills in all stages from a complete U-shaped opening to a terminal one which is always circular, I am led to believe that these structures increase in number throughout the greater part, if not the whole, of the life of the animal. The greatest number of slits which I have observed was fifty-seven pairs. Figures illustrating the development of the branchial



skeleton, &c., will be given when the histology of the gills is described.

Together with the increase in number of the gills the differentiation between the digestive and intestinal region becomes more prominent, the bright yellow-brown of the former showing through the transparent body wall, being a most striking feature in the appearance of the animal. When first perceptible, the digestive tract is a simple tube, separated by a slight constriction from the intestine. As growth proceeds this constriction becomes more marked, and when the second gill-slit is fully formed the separation between the two is sharply defined (fig. 2). Subsequently a fold arises in the digestive region which gives it the appearance of being made up of two saccules (two gill-slits). This condition becomes more and more marked, and then a third saccule appears posteriorly (4—5, *gs.*). When, however, the animal is seen from the dorsal side the alimentary canal is seen to have a wavy contour, the two saccules being thus parts of a slightly bent tube. Moreover, in longitudinal sections the divisions between the saccules are parts of a spiral fold which traverses the whole digestive region. When five gill-slits are formed there are three saccules, and in animals with ten gill-slits they are five in number. After this the body walls become much more opaque, attaining the condition which they present throughout adult life. It is consequently not possible to follow the internal development after this stage by means of surface views.

The walls of the intestinal region are also thrown into folds, but their arrangement would appear to be irregular. The cells in this tract bear long flagelliform cilia which appear to drive a current through the anus.

The anus is first found at about the time of the formation of the second gill-slit. As previously mentioned it is almost if not quite in the position in which the blastopore closed, being posterior, median, and dorsal. When the tail is formed the anus is immediately dorsal to it, in fact, its ventral margin is formed by the dorsal side of the tail. In ordinary conditions

the anus remains open widely, but when the animal is irritated it contracts its body and draws in the intestine, closing the anus, over which there project two flaps of the body wall. These flaps are very thin and transparent presenting an appearance as of a posterior vesicle (fig. 3a).

In some specimens a curious separation between the mesoblast and epiblast occurs in this place, which may be due to re-agents or may have some significance; this structure will be treated of together with the other formations in the third body cavity.

In the transparent animal pulsatory contractions can be seen in a vesicle lying on the dorsal side of the notochord, but owing to the imperfect transparency of the body walls in this region nothing more could be definitely affirmed as to the course of the blood. As will be seen in considering the internal structure, a large trunk appears (2—3, *gs.*) in the dorsal mesentery; pulsations could also be observed in this structure, which seemed to pass from behind forwards, but occasionally an appearance was produced as of a reversal in the direction. But in consideration of the fact that the ventral wall of this vessel is by the nature of the case adherent to the splanchnopleura, while the dorsal wall was fixed in the somatopleura, no very certain importance can be attached to any observations of pulsation in the dorsal vessel, since any peristalsis in the gut might produce this appearance. The same applies to the ventral vessel, which is said to be contractile in *B. minutus* (Spengel). On the whole, however, the balance of evidence was distinctly in favour of postero-anterior pulsations in the dorsal vessel. No corpuscles were discovered in the blood which is colourless. In preserved specimens it appears as a homogeneous coagulum, which in specimens preserved in Perenyi's fluid shows a slight tendency to granulation.

Large amœboid-looking cells are visible, floating about in the body cavities, especially in the second.

After about seven to eight gill-slits are formed the general look of the animal changes, mainly owing to the fact that the walls of the body become more and more opaque. This seems to be

due to thickening of the ectoderm and the appearance of numerous mucous glands on the skin. The whole skin is uniformly ciliated from the time when the blastopore closes throughout life.

At about seven to eight gill-slits the suctorial tail disappears, probably atrophying rapidly, but as to this process nothing more can be predicated. It is to be found in some larvæ with eight gill-slits, while others in the same stage are without it. The anus is then terminal, circular, and permanently open.

At ten gill-slits the ovaries are first perceptible, but as yet are not marked enough to appear in a surface view. In older animals they form large yellowish-grey projections from the sides of the body. Their minute structure, together with that of the testis, will be given later.

The body of the adult is very highly coloured, the proboscis being of a yellowish-white tint. The collar is a brilliant red orange (especially in males), with a white line round the edge of the operculum, while the rest of the body is of an orange yellow, shading to pale green yellow in the intestinal region, which is semi-transparent throughout life. The distinction between the colour of the males and females is very well marked in *B. Kowalevskii*, the genital regions being grey in females and yellow in males. The sexes are of different colour in all the Enteropneusta, most prominently so in *B. salmoneus* (Giard), in which the males are chrome yellow and the females salmon coloured.

It may be well, before passing to the internal development, to mention the peculiar odour which the creatures possess. This odour is very penetrating and persistent, resembling that of chloride of lime with a fæcal admixture. All the species of Enteropneusta which I have examined alive possess more or less offensive odours. This peculiar property is most developed in *B. Brooksii* (new species), in which the smell is very distinct after the animals have been months in spirit, which has been often changed. The smell of this species is strongly suggestive of iodoform. It is so powerful as to be a considerable drawback to investigating the species.



Another feature which ought not to be overlooked in a general account of this species (*B. Kowalevskii*) is its extreme vitality. In a bucket of unaërated water in which all other animals had died some days before, in a hot climate, these creatures were able to carry on their existence, and parts of the body may be seen moving about by means of the ciliated skin to which a completely macerated skeleton of the branchiæ is attached. Lobes of the testis, torn off, will likewise swim about for days. To what extent the body is capable of regeneration I cannot say. Specimens were found in which there was at all events an appearance suggesting that the proboscis had grown again. Spengel has alluded to regeneration of tissues as occurring in *B. minutus*, and I have little doubt that it is also common in *B. Kowalevskii*.

With regard to the specific name of this form, it appears that the figure and description given by Agassiz of *B. Kowalevskii* identify it with the form which is the subject of this paper. The mode of development ascribed by him to the species is of course entirely different. Seeing, however, that he was unable to show the connection between the animals found by him in the beach and the *Tornaria* which he reared, it does not seem by any means certain that these *Tornaria* were the larvæ of *B. Kowalevskii*. On the whole, it is at least possible that they were the young of some other species, *e.g.* *B. Brooksii*, which occur at least as far north as the Chesapeake, and probably higher still on the coast.

From a general survey of the group Enteropneusta, which I hope subsequently to attempt, I think it will appear likely that *B. Kowalevskii* stands, in many respects, in a group differing in several features from the other members, which agree with one another in these points, *e.g.* short proboscis, complicated branchial skeleton, operculum small, liver saccules present, eggs minute, &c. It is to the latter division I am inclined to believe that *Tornaria* alone belongs.

In studying the anatomy of *Balanoglossus* by means of sections difficulty arises owing to the variable amount of con-



traction which the body may undergo in preservation. The trouble chiefly occurs in the case of the proboscis-stalk and folds of the collar. By comparing figs. 3 and 4, which were drawn from living specimens in the extended state, with fig. 5, which is taken from a preserved specimen, these relations will be understood. In the contracted animal the gill-slits are always more or less obscure, owing to the great shortening which takes place in the branchial region, together with the protrusion of the valves (fig. 5, *vlv.*).

In older animals this contraction is not nearly so great, probably owing to the increased firmness of the branchial skeleton.

#### Internal Structure.

Stages F and G—Skin.—The ectoderm is composed of long fusiform cells arranged two to three deep over the body, except in the dorsal side of the collar groove, where they are columnar and one layer thick. Also in the posterior dorsal region the skin is thinner than that of the rest of the body. The whole surface is ciliated. Beyond the fact that the cells are more compressed, and closely arranged, the structure is similar to that of the previous stage.

Nervous System.—The solid cord which began to separate from the skin in the middle dorsal line at Stage F continues to sink inwards. No lumen is as yet present in it. Throughout its length it still remains in contact with the skin, fusing with it at both ends (figs. 10 and 20—24).

Towards the end of Stage G a differentiation begins between the upper and lower parts of this cord, the upper being formed of cells, while the lower part consists of lightly stained substance, which in older animals is distinctly made up of fibres. Its fibrous nature cannot in this condition be certainly affirmed, probably owing to defect in preservation. The formation of a nervous network over the whole body, which afterwards occurs, is not yet begun.

Hypoblast.—The mouth is ventrally directed (fig. 7), and

the anterior wall of the gut (Stage E to F) runs at right angles to the long axis of the body. As will afterwards appear this feature is of importance. In longitudinal section, a commencing differentiation between the branchial and digestive region is perceptible. The cells of the former are columnar, while those of the latter have irregular amœboid processes which give the inner wall of the gut an irregular contour. The anus is not yet formed.

In the front end of the third segment of the larva (Stage F), anterior to the ring of cilia, the sides of the gut give rise to a pair of dorso-lateral evaginations; these pouches are the first indications of the gills. No change has occurred in the skin covering them. Subsequently they come in contact with the skin, the walls fuse and then a perforation is formed through the fused portion, apparently occurring by a process of degeneration of the tissue. Fig. 29 is from a section taken through the side of one of these evaginations. The subsequent appearances are shown in figs. 41 and 42, which are from an older larva.

**Notochord.**—In the later stages of F and G in the anterior dorsal wall of the gut, arises a most remarkable structure. For reasons which will appear when its later development and fate is considered, I propose to compare this organ with the notochord of the Chordata, and by this name it will be subsequently spoken of.

In Stage E it was stated that the anterior wall of the hypoblast came vertically to join the skin at the mouth (figs. 7 and 10). As, however, development proceeds, the dorsal wall of the pharynx becomes partly constricted from the remainder (figs. 20 and 22). As this process of separation of the dorsal wall proceeds, the part so separated grows forwards so that it comes to project slightly in front of the anterior end of the gut (fig. 30). By this means a hypoblastic tube is formed dorsal to the gut, with a lumen which opens into the archenteric cavity (figs. 21, 22, and 30).

**Mesoblast.**—The lining of the anterior body cavity in Stages E and F is composed of rounded cells arranged in cou-

tact with the ectoderm. These cells are in some parts only one layer thick (anterior and posterior walls) (fig. 8), while in others (ventrally) they proliferate rapidly (fig. 9), forming loose masses of cells, the outer elements of which are elongated, with rounded heads from which the spherical cells which form the inner portion are budded. This proliferation continues until the proboscis cavity is partially filled up. But in the later phases of Stage F elements are formed other than the rounded cells above mentioned, in the shape of fibres (fig. 13) which appear to arise in a curious way, as is shown in figs. 9, 10, 12, &c. The elongated cells gradually become pyriform, the round ends being for the most part central, while the fine ends are drawn out into peripheral fibres. The round heads then appear to separate from the fibres, so that in examining the mesoblastic structure lining this cavity in late larvæ of Stage G, the elements are arranged in the following order: centrally, a small empty cavity surrounded by a ring of spherical granular cells; next a layer of pear-shaped cells continued into peripheral fibres, and externally a layer, composed almost, and later in life entirely, of radial fibres. Some of these are inserted into the lower layer of the skin, and are probably a peculiar form of connective tissue. In the heads of the pyriform cells brightly refractive granules may be seen; whether these are food or waste products cannot be affirmed.

Such then is the lining of the proboscis-cavity. In the anterior third it is evenly distributed over the inner surface, but at the back of the posterior third, where the proboscis tapers abruptly to its stalk, the layer of mesoblastic tissue is much thinner dorsally than laterally and ventrally (compare fig. 13 which is through this region with figs. 12 and 11 which are anterior to it). On passing further backwards, the cavity in Stage G is divided into two by a great proliferation of mesoblast from the dorsal surface, which grows downwards until it meets the ventral mesoblast. The position occupied by this structure at first coincides with the point at which the anterior mesoblastic pouch closed off from the archenteron. In that stage the anterior body cavity was a simple sac con-



tinued backwards into two lateral horns. The mass of cells which now arise at the original point of separation, therefore, constitutes a continuation of the division between these two horns into the anterior simple cavity (fig. 14). As will shortly be seen, this division of the back of the anterior cavity into two is correlated to the forward growth of the notochord.

In this septum, which is composed of roundish, hexagonal cells containing many granules (fig. 16), appears the first rudiment of a peculiar organ which subsequently is a conspicuous and characteristic structure in the proboscis of all the Enteropneusta, viz. the proboscis-gland ("heart" of Spengel<sup>1</sup>). This gland has at first the relations shown in fig. 10, *gl*. It consists (Stage F) of a triangular mass of loose tissue containing nuclei in which but few cell-outlines can be seen, and would appear to be formed by a sort of degeneration of the mesoblast of the septum. As yet it contains no cavity. Immediately behind and ventral to it is the anterior end of the notochord (fig. 17).

Fig. 18 is taken through the posterior apices of the mesoblastic horns behind the gland.

Middle Body Cavities.—These are (Stage E) a pair of simple cavities divided by a dorsal and a ventral mesentery, completely closed from both the anterior and posterior cavities, as they remain throughout life. They are lined by round or crescentic mesoblast cells. As the proboscis-stalk is constricted, the anterior parts of these cavities are compressed into two forwardly directed horns. The horn of the left side is shown in fig. 18. From an early period it projects in front of that of the right side.

In Stage F a histological differentiation occurs in the splanchnopleure at the place of union between that part of the hypoblast which is destined to form the notochord and the lower section of the pharynx.<sup>1</sup> This appearance is shown in fig. 25, *x*). It consists in the prolongation of the ends of the

<sup>1</sup> For reasons which will subsequently appear this term is somewhat inappropriate.



mesoblast cells which are in contact with the hypoblast into curious tails, which are refractive.

I was at first led to suppose that these tails were muscular, and this undoubtedly is the fate of many of the mesoblastic elements of this region, but no direct evidence of the contractile nature of these pear-shaped cells was attained beyond the general suggestion of their shape; on the other hand, when the notochordal sheath is developed in this region, an appearance is presented which suggests the possibility of their having taken part in its formation. Their histological characters are, however, strikingly similar to those of the cells which occur at the sides of the notochord in the same region in *Amphioxus* at the time when it has eleven pairs of mesoblastic pouches (Hatschek, No. 4, figs. 124, 126, &c.). These cells are stated by Hatschek to be muscle-fibres; by analogy it seems, therefore, likely that this may be the real nature of the same cells in *Balanoglossus*.

As development proceeds, proliferations of mesoblast are formed in the ventral region of the middle body cavities. From each side in the posterior region of these cavities a tubular portion is separated off from the rest (fig. 28).

The fate of these parts is not quite certain. It seems, however, likely that they unite with two forward growths from the posterior body cavities to form the tissue space in which the dorsal blood-vessel is ultimately enclosed throughout the collar region. This tissue space I propose to call the perihæma cavity (fig. 60, &c., *Ph. c.*).

The posterior body cavities are simple cavities, similar to the middle pair. The dorsal and ventral mesenteries persist throughout life. As yet they contain no special differentiations.

#### Period between the Formation of the First and Second Pair of Gill-Slits.

**Skin and Nervous System.**—The histology of the skin in the proboscis and collar regions has not undergone material

alteration since the last stage. The epiblastic cells are somewhat smaller and more closely packed. In the posterior regions, however, the ectoderm is thinner than in the younger animals, owing to the rapid growth which occurs at this time in the trunk region (fig. 46). Unicellular mucous glands occur at rare intervals in it. But in the lower layer of the skin at the posterior surface of the proboscis is formed the beginning of that network of nerve-fibres which is such a prominent feature in these regions of the body in later life. Though a network of this kind eventually is formed on the inner surface of the skin all over the body to a greater or less extent, it is as yet only to be seen in the base of the proboscis. The exact process by which this layer is deposited is not certain, but it would appear that cells of the inner layer elongate and form multipolar cells with long, thread-like, anastomosing tails (fig. 32).

At this stage nuclei are still visible in this fibrous layer, though in later stages they have almost entirely disappeared from it (fig. 54, &c.). From this point in development onwards these fibres constitute a perfectly defined layer of tissue. Projecting into it may be seen some of the fibres which were described as being formed from the mesoblastic lining of the proboscis cavity. These fibres are presumably supporting structures. Occasionally an appearance is presented as of an anastomosis occurring between them and the tails of the nerve-fibres. Whether this is really the case or not, it can scarcely be doubted that the muscle-fibres, which are now forming in the proboscis cavity, receive their innervation from the fibrous layer of the skin, to which many of them are attached, and thus such an anastomosis is not *à priori* improbable. On the other hand, the structure of the mesoblastic fibres is rather indicative of a supporting than of a contractile function. But, as will afterwards appear, there are eventually present in the mesoblastic elements of these animals cells which present almost every shade of variety between undoubted contractile fibres and obvious connective tissue, so that it is by no means easy to determine the nature of these fibres with precision.

On the whole I am inclined to regard them as supporting structures.

The separation of the dorsal nervous system is much more marked during this period than it was before it. It is now completely separate from the point of junction of the proboscis with the trunk to almost the level of the first pair of gill-slits. At its anterior end (fig. 36) may be seen the beginning of the process by which the anterior lumen is formed. This is effected by a forward growth of the collar, together with a continual sinking and horizontal invagination of the nerve-cord.

This lumen, thus formed, never extends for more than a short distance into the cord, which, however, in its middle and posterior regions in older animals, contains remarkable spaces lined by columnar cells, more or less separated from each other by strands of tissue, which will be described, together with the later development and histology of the nervous system.

The nerve-cord, as always, fuses with the skin at both ends, but from its posterior point of junction the rudiment of its dorsal continuation in the skin may already be seen in section as a small area of fibrous tissue in the base of the skin in the middle dorsal line (fig. 42). A similar strand (fig. 42) may also be seen on the ventral side, beginning a little in front of the first gill-slits. The two cords are still quite unconnected.

**The Proboscis Pore.**—The first appearance of this structure is a thickening on the inner surface of the epiblast in the proboscis stalk, which soon becomes hollow while still attached to the skin (fig. 34, *p. pr.*). This epiblastic sac is from the first asymmetrical, being on the dorso-lateral aspect of the left side. From the first, the cells of which it is formed are columnar, and it has no communication as yet (two gill-slits) with the exterior or with the body cavity.

### Hypoblastic Structures.

**Branchial Region and Notochord.**—The process by which the mouth comes to be forwardly directed has already been described. In larvæ with one to two gill-slits it has already



begun (fig. 45). The walls of the branchial region are distinctly differentiated from those of the rest of the gut, consisting of long, solid-looking cells arranged in layers of one to two deep. The lumen of the gut is very small anteriorly and has an irregular outline in preserved specimens (figs. 36 and 37), but in the middle of the collar region as at present marked out, its lumen is continuous dorsally with that of the notochord (fig. 39).

This notochord, which is now a very prominent feature in sections of the anterior end of the body, arose in the first instance, as already stated, by a forward growth of the anterior dorsal wall of the pharynx, which thus shuts off a short diverticulum of hypoblast (fig. 30). The part of the pharynx with which the walls of this diverticulum are continuous, then separates itself from the rest by longitudinal constriction, which at first causes the lumen of the gut to take an 8-shaped figure, the separation of the dorsal part of the 8 becoming finally complete from before backwards. This process gives rise to the appearance seen in fig. 37. The part thus constricted off becomes then entirely separated except at its posterior end, where throughout life its lumen opens into the pharynx.

In its anterior region the lumen of the notochord is always suppressed at this stage, owing to the compression of the ventral against the dorsal wall. Moreover, in larvæ of this, as of all subsequent stages, the lumen is altogether obliterated in part of its course. This obliteration does not appear to occur progressively from before backwards, but more or less irregularly, so that, as in fig. 38, the lumen may have already disappeared while still present in a region anterior to this (fig. 36). As, however, in older animals the lumen is always continued far into the notochord of the proboscis cavity (namely, to a point anterior to that where it is already obliterated in two-gill larvæ), it is almost certain that the subsequent increase in the length of the notochord is due to a growth from behind forwards, and that all the notochord which is as yet formed (two gill-slits) is pushed bodily forwards by a proliferation, probably occurring at the point of union with the gut. The



alternatives, that the growth occurs at the apex or at any point intermediate between the two ends is unlikely, from the fact that almost immediately after two gill-slits the tissue of which it is composed becomes vacuolated and irregular, undergoing the "degeneration" characteristic of notochordal substance, presenting therefore by no means the appearance of a growing tissue.

The length and proportions of the notochord at this stage are indicated in fig. 45, which is, however, not a truly median section. Its anterior end already projects far into the anterior body cavity, pushing in the mesoblastic lining. Fig. 45 is from a specimen slightly older than that from which figs. 37, &c., are taken, and the commencing degeneration of the notochord tissue is already begun.

To recapitulate: the growth of the notochord is due to:

1. A forward growth of the dorsal anterior portion of the archenteron (fig. 30). This is supplemented by—

2. A longitudinal constriction of the dorsal region of the pharynx, which gradually travels backwards (cp. figs. 21 and 22 with figs. 38 and 39), separating a hollow hypoblastic tube which remains open to the gut behind.

3. A forward growth from the point of junction with the gut.

In connection with the notochord must be mentioned the skeletal rods, which now just appear, though it cannot be positively affirmed that they are of hypoblastic origin. When first visible, they are two short rods of a deeply-stained, structureless substance, which lie in the angles between the notochord and the dorsal wall of the pharynx. As first seen in this position they appear to be formed externally to the hypoblast cells, against the ends of which they lie. Their posterior ends are enclosed in the hypoblast (fig. 39), and it is difficult to understand how this can have been brought about if they were secreted by the mesoblast cells. This would involve an outward growth of the hypoblast to inclose them, of which there is no appearance. As will afterwards be seen the view that they are of hypoblastic origin is supported by the fact that they continue growing with the growth of the animal, and that their

thickness is, so to speak, inversely proportional to that of the cellular tissue of the notochord, which becomes thinnest in the region where they attain their maximum size. This, therefore, suggests that they are formed at the expense of the notochord. An analogy moreover at once occurs of the secretion of such a substance from notochordal tissue in the case of *Amphioxus*, in which discs are deposited of very similar histological character to these masses in *Balanoglossus*. These two rods posteriorly bend downwards and then slightly forwards lying in the hypoblast. They are therefore each cut twice in sections through this part of the body.

Behind the end of the notochord are the gill-slits, which are still only circular pores leading to the exterior (fig. 43). The lumen of the gut in the branchial region is (in contracted specimens) much suppressed, and its ventral side, however, always is grooved, and in this groove the cilia which line the branchial region are well developed.

When the animal contracts, the branchial region of the gut posteriorly projects over the front of the digestive region on the dorsal side (fig. 44).

The digestive region is quite distinct from this point in development onwards. Its cells have the appearance shown in fig. 45, being large cells with amoeboid processes containing large granules. From the back of the digestive region the intestinal region is now marked out. Its walls are thinner, and the cells composing it are long and ciliated at their inner ends. The anus is a large aperture, permanently open when the animal is expanded, situated dorsal to the tail. There is no epiblastic proctodæum.

### Mesoblastic Structures.

**Anterior Body Cavity.** The mesoblast of this tract may now be divided into two parts—(1) a peripheral portion which lines the body walls of the proboscis, and (2) a central portion which is pushed in by the forward growth of the notochord; between these two portions there is a body cavity which retains a clear central space throughout life.

(1) The peripheral part consists of cells and fibres. The cells are mostly pyriform similar to those of one-gill larvæ. They contain few granules and are much reduced in number. The fibres are more numerous. They are of several kinds: thick strands that are obviously muscular, running as yet only in a longitudinal direction, having their ends inserted in the skin: and also thinner fibres, which are arranged circularly, as in the periphery of the middle third; longitudinally, only occurring as a sort of sheath separating the circular fibres from the general connective tissue, and occasionally in the central portions; radially, as over the whole periphery of the proboscis cavity, and finally, very fine fibres forming a loose network connecting all the mesoblastic elements together. As may be seen in figs. 31, &c., there is as yet no suggestion of the peculiar concentric arrangement of the longitudinal fibres, which gives a section of the adult proboscis its curious appearance. The radial fibres are mostly inserted into the skin (fig. 32), their possible connection with the epiblast has been already discussed.

There are still present a few of the large spherical cells which formed the inner layer of mesoblast in one-gill-slit larvæ, but they contain fewer granules, and are only found in the posterior parts of the cavity.

(2) The central portion in the one-gill-slit larva was made up of a mass of spherical and polygonal cells surrounding a central part filled with loose tissue (fig. 16). As the notochord grows forward, this structure, which, from its subsequent fate may now be termed the proboscis gland, is prolonged with it. As this forward growth occurs, a basement membrane forms between the mesoblast outside the proboscis gland and the loose tissue contained in it. Fig. 46 shows a section anterior to the part where this basement membrane is formed. The mesoblastic cells are here large and granular, having irregular shapes. The proboscis gland now is hollowed out, so that it contains a space which extends from the proboscis stalk to the front end of the notochord. This space contains a few mesoblastic cells, which are as yet not obviously differentiated.



The position of this space is shown in fig. 45. It will be seen in the sequel that the mass of the secreting tissue of the gland is formed from the cells covering this space, and forming the sides of this central portion of the mesoblast. The space itself contains eventually but few of these secreting cells, and will be spoken of as the sac of the proboscis gland (fig. 52, *gl. s.*).

The heart is as yet not represented.

**Middle Body Cavities.**—The tissue lining these cavities does not exhibit more than a general progress of differentiation. Owing to the increased narrowing of the proboscis stalk the two anterior horns of the cavities are more distinct. In the dorsal and ventral mesenteries basement membranes occur. The cells lining these cavities are generally pyramidal or crescentic, some of them being radially directed and fusiform.

**Posterior Body Cavities.**—The tissue of the posterior mesoblastic pouches has undergone the same proliferation and progressive differentiation as that of the middle cavities. These processes are not, however, quite so far advanced. The two horns (peri-hæmal cavities) which began to grow forwards above the gut in the one-gill larva are now much more developed. They now extend into the back of the collar region, in front of the first gill-slit. They are filled more or less with loose mesoblastic tissue containing a few fibres. As before stated, in the mesentery between them is formed the dorsal blood-vessel. This structure appears as a split in the mesentery, and is as yet quite empty in preserved animals. This split extends already through the whole course of the perihæmal cavities. On the ventral side also a split is formed in the lower mesentery of the posterior body cavity to form the ventral blood-vessel. There is as yet no connection between the dorsal and ventral vessels.

From this point the details of the subsequent development and anatomy of the parts will be given in the section dealing with the separate organs; but, before doing so, it may be well to describe briefly the general course of the later history of the internal structures.

**Notochord.**—As will be seen, this structure increases



greatly in size, and assumes a vacuolated appearance closely resembling that of the notochord of young Lampreys and Elasmobranchs.

The skeletal rods attain a considerable size. Their anterior ends unite, forming a single bar, while their posterior ends diverge, partially enclosing the gut. This whole structure forms the support of the proboscis.

From its development, position, relations to surrounding parts, histology and function it appears to me to be comparable with the notochord of the Chordata, and this name is strictly appropriate to it. Even if the suggestions which will be made hereafter as to its phylogenetic significance be not accepted, this rejection would in no way militate against the fact that this structure is to all intents and purposes a notochord, which can only be designated as a longitudinal dorsal supporting rod, derived from the hypoblast.

The nervous system afterwards attains a great development (fig. 60). The dorsal cord in the collar sinks further and further from the skin, being (in *B. Kowalevskii*) connected to it by a mesentery. The lumen is in this form less developed than in *B. minutus*, &c. The ventral cord is the next to appear, and almost simultaneously with it arises the deposit of nervous tissue in the skin at the base of the proboscis. This deposit afterwards attains a great extent, forming a thick band round the proboscis stalk. It may be noticed that this nerve-ring has practically the same relation to the proboscis that the ring of ganglia in Nemertines presents, the proboscis of *Balanoglossus* being, however, permanently protruded, and the nerve-ring still in the skin. Both these nerve-rings agree in being traversed in Nemertines by two and in Enteropneusta by one pore communicating from the exterior to sacs which were originally archenteric diverticula.

**Body Cavities.**—As before mentioned, the left horn of the anterior body cavity comes to open by the proboscis pore to the exterior. This opening is median and dorsal in other species, but in *B. minutus* it is on the left side throughout life. In all species it perforates the nerve-ring of the stalk.

Nearly all the proboscis cavity is eventually filled up with loose tissue. This is composed of a number of concentric rings of longitudinal fibres and connective tissue. These rings attain the maximum number of eight. In fig. 51 the general appearance of an older proboscis cavity is shown. The concentric arrangement is, however, not yet attained in the stage there figured.

A free space is always present between these rings of tissue and the central structures in preserved specimens.

The proboscis gland becomes a large mass of tissue composed of anastomosing blood-vessels covered with conical cells fixed on the vessels by their apices. Many of these cells contain remarkable yellow granules, which are also to be found outside the cells, sometimes presenting a conglomerate arrangement. They would seem to be formed in the cells and thrown out. They are also to be found in the sac of the proboscis gland. This sac is blind posteriorly, but anteriorly the loose tissue which it contains passes into unbroken connection with the remarkable cellular layers covering the blood-vessels. Hence the sac is in communication with the central body cavity through the tissue spaces of the gland. The function of this gland is quite unknown. Spengel suggests that it is an "internal gill." It does not seem probable to me that an animal with some sixty pairs of true branchial clefts would also possess another large and complicated organ of entirely different structure also for respiratory purposes. The presence of the brown granules suggests that it may be excretory. If this were so, the excreta might be expected to pass out by the proboscis pore which opens into the cavity in which the gland lies. No direct evidence was obtained as to the normal direction of the flow through this pore. Spengel and other observers state with regard to *B. minutus* that water is taken into the body cavity at the proboscis pore, but my own observations do not confirm this statement. On the contrary, particles of Indian ink or carmine held in suspension in the water in which the animals have lived for days, cannot be found to enter the proboscis cavity, while similar particles,

if placed in the tissue spaces of the proboscis, are certainly expelled by the pore. This evidence does not of course demonstrate, beyond doubt, that inwardly directed currents never enter the pore but only gives a presumption against them.

Spengel's statement of the absence of the pore described by Kowalevsky and Agassiz, at the apex of the proboscis, is true for all the species which I have examined.

The Heart.—As mentioned by previous observers, a large vesicle may be seen pulsating above the water-vessel in *Tornaria*; such a pulsation may be observed in the dorsal side of the base of the proboscis in *B. Kowalevskii* at the stage of two to three gill-slits. Spengel states that this contractile sac is the upper of the two cavities lying above the notochord (figs. 51, 53, &c.); this he calls the "heart." In consideration of the fact (which he also admits) that it contains no blood, gives off no vessels, and has no muscular walls, this name seems open to misconstruction. As this so-called "heart" is merely a space filled with loose tissue which is part of the proboscis gland I have preferred to call it the sac of the proboscis gland, and to reserve the name "heart" for the sac which lies between this space and the notochord (figs. 50 and 51, *ht.*). That this is the actual heart can I think hardly be doubted. It arises at about three gill-slits as a single horizontal split in mesoblast between the notochord and the sac of the proboscis gland. It acquires muscular walls and is always nearly full of a coagulum similar to that which is found in the remaining blood-vessels of the body, which can all be traced into connection with it.

These peripheral vessels are (1) a longitudinal dorsal one, running from the heart to the tail in the dorsal mesentery from the back of the collar, and in the collar as a blood-space surrounded by the perihæmal cavities (fig. 60); (2) a ventral longitudinal vessel running from the back of the collar to the tail in the ventral mesentery. These two are connected by blood sinuses in the skin and in the wall of the gut. I have not seen the definite circular vessel which other observers state



surrounds the gut anteriorly. The principal skin sinuses are a pair of large ones which extend on each side of the dorso-lateral regions of the proboscis (fig. 51).

The Collar Pores.—On the outer wall of each atrial cavity appears a thickening at about eight gill-slits. This thickening acquires a perforation which leads from the collar body cavity to the atrial cavity. These perforations acquire a curious folded lumen and become ciliated constituting the collar pores. Their opening into the atrial cavity is continuous with that of the first gill-slit. From analogy it may be expected that these pores are of an excretory character. With regard, however, to the direction of the flow through them, the evidence is as unreliable as that as to the currents in the proboscis pore. Spengel states that water is taken into the body cavity at these points, while I was unable to find that coloured particles ever entered it. Similarly, however, such particles placed artificially in the collar body cavity were washed out at these points.

The Middle and Posterior Body Cavities.—These cavities become in adult life more or less filled with connective tissue, &c. The cavity of the middle pair becomes practically obliterated owing to the great development of loose tissue in it. But in the posterior cavity this proliferation is never so great. The middle pair of body cavities is far more choked up in *B. Kowalevskii* than in *B. minutus*, but in *B. Brooksii* the amount of connective tissue is even greater. This fact is interesting in the present state of views as to the morphological meaning of "coelom," as presenting an example of a body cavity arising in a most typical "mesodermic" manner, assuming ontogenetically precisely such an appearance as is presented by the "mesenchyme" of *Platyhelminths*, &c.

A statement as to the origin of the generative organs is reserved for the present, as some doubt exists as to the layer from which they are derived. The general appearance is, however, suggestive that they are of epiblastic origin.

Before beginning a detailed account of the later development



it may be desirable to discuss briefly the new light which these facts throw upon the affinities of the Enteropneusta.

In 1881 Metschnikoff published a detailed comparison of *Balanoglossus* with the Echinoderms, comparing *Tornaria* with *Bipinnaria*, showing that the resemblance is close, and concluding with the suggestion that *Balanoglossus* should be included among the Echinodermata in a separate division, "Bilateralia." The branchial structures he compared to the openings from the body cavities of Echinoderms. This view, as thus expressed, receives no support from further observations, and would now appear to be untenable.

As mentioned above, all the Enteropneusta possess a supporting structure which is comparable with the notochord in every way, except in extent and in the persistence of its connection with the alimentary canal. Its resemblance to that of *Amphioxus* is especially striking, for in *Amphioxus* the notochord projects a long way in front of the mouth. It moreover possesses gill-slits which are not only without parallel, except among the Chordata, but also in structure, position, and development, agree exactly with those of *Amphioxus*, in which the slits acquire the same U-shaped form.

The agreement in the position of the blood-vessels and skeleton of the gill bars is also very close. The fact of their gradual increase in number from before backwards throughout life is another common feature.

The position and mode of origin of the central nervous system is also similar in both forms; the invagination of the dorsal cord in *Balanoglossus* being, however, only partial, while that of *Amphioxus* is complete.

The mesoblastic pouches suggest the same resemblance, differing only from those of *Amphioxus* in number, being one median and four lateral, while those of *Amphioxus* are one median and twenty-eight lateral. As I have already pointed out, the fate of this anterior pouch is in the two animals closely similar. In both it is divided into two as the notochord grows forward. In *Amphioxus* the division is complete, while in *Balanoglossus* it is partial. In both, the backwardly-projecting

horn upon the left side becomes lined by ciliated columnar cells, and opens to the exterior. Moreover, in both animals this opening has a definite relation to the nervous system. In *Amphioxus* it becomes the "olfactory" pit (Hatschek), while in *Balanoglossus* it is surrounded by a mass of nervous tissue. Finally, the collar folds, especially of *B. Kowalevskii*, would appear to be comparable with the commencing atrial folds of *Amphioxus*, for the most anterior gill-slits open into the cavity which is thus enclosed.

The pair of ciliated funnels opening from the collar body cavities to the atrium has been compared above to the excretory tube mentioned by Hatschek in a similar position in *Amphioxus*.

A pair of tubes has been described by Lankester in *Amphioxus* opening into the back of the atrial cavity, communicating with the dorsal body cavities. It may be remarked that if the collar fold of *B. Kowalevskii* were prolonged backwards, as the atrial folds are in *Amphioxus*, the two collar funnels would then be carried backwards, and have relation similar to that of these tubes, which, as suggested by Lankester, may be excretory.

To recapitulate: striking resemblances to the Chordata, and especially to the Cephalochord type, are to be found in the following structures:

- (1) The notochord.
- (2) The gills and branchial skeleton and blood supply.
- (3) The central nervous system.
- (4) The origin of the mesoblast.
- (5) The peculiar fate and remarkable asymmetry of the anterior pouch.
- (6) The atria.
- (7) The excretory funnels.

In each of these cases, excepting that of the branchial structures and the excretory funnels, the condition is that which would be produced by a partial or arrested development of the corresponding structure in *Amphioxus*.

The above considerations appear to justify us in including

the Enteropneusta among the Chordata. I would, therefore, tentatively suggest the following table :

Chordata.—Hemichordata (Enteropneusta).  
                   Urochorda (Ascidians).  
                   Cephalochorda (Amphioxus).  
                   Vertebrata.

It is not now proposed to enter into a more detailed discussion of the morphology of the group, or of the light which an acceptance of this suggestion throws on the origin of the Chordata. A fuller examination of these points is reserved for a subsequent occasion.

It may nevertheless be advisable to point out that since, according to Spengel, the tissue of the "water vessel" of *Tornaria* forms the lining of the proboscis cavity of *B. minutus*, this "water vessel" is therefore the same structure as the anterior body cavity in the form just described. If, then, the "water vessel" of *Tornaria* is comparable to the "water vessel" of *Bipinnaria*, which has a similarly asymmetrical development upon the left hand side of the body, which view has been held by all previous observers, it would therefore appear to follow that the water vessel of *Bipinnaria* is *primâ facie* comparable with the asymmetrical anterior body cavity of *Amphioxus*.

### Later Development and Comparative Account of the Organs in the various Species.

The species which I have examined are the following :

*B. Kowalevskii* (Alex. Agazziz.) (Coast of North America).

*B. Brooksii*, n. sp. (ditto).

*B. minutus* (Kowalevsky.) (Bay of Naples).

*B. salmoneus* (Giard.) (Iles de Glenans, off South Coast of Brittany).

*B. Robinii* (Giard.) (ditto).

*B. Kowalevskii* differs from all the others in having—

- (1) a relatively long proboscis ;
- (2) no hepatic sacculations ;

- (3) a simple branchial skeleton, not connected by longitudinal bars, as in the other forms;
- (4) very short collar funnels, the external opening of which is directed transversely instead of posteriorly, as in the others, in consequence of
- (5) the greater extent of the backwardly-directed atrial fold.

As far as can be determined from Agassiz' account, his species agrees in these points with the one which is the subject of this paper.

### The Notochord and Axial Skeletal Rods.

B. Kowalevskii.—The general course of development of the notochord has been already described. Fig. 47 shows the histological characters of the cells at two gill-slits, when they are still large full-looking cells with large nuclei.

Fig. 48 is from a section of the proboscis stalk in the region of the pore of a larva with three gill-slits. It exhibits the commencing degeneration of the notochordal tissue and the increase in size of the structureless deposit which constitutes the skeletal rods.

In this region the skeletal rods unite to form a single median rod, which is continuous with the notochordal sheath.

In figs. 49—53 the appearance of the notochord at four gill-slits is illustrated. The degeneration is now far advanced. Nuclei are rare in the notochord, and the cells are vacuolated, as shown by the fact that the nuclei occur in the nodes of the cell outlines. The protoplasm of the cells merely forms a kind of network containing a few nuclei. The remainder of the space is probably occupied by some homogeneous non-protoplasmic substance, such as may be supposed to fill up the notochordal tissues of other forms.

Figs. 49—52 are from sections taken in front of the lumen (cp. fig. 57). In fig. 53 the lumen is reached. It will be observed that the lumen at this point still ends as a fine tube. In later life a great thickening of the notochord takes place at this point, and the lumen then acquires a downward extension



(figs. 57 and 56). Immediately behind this downward extension lies the anterior end of the united skeletal rods, which here attains its greatest thickness, almost filling the sheath of the notochord, the tissue of which is here almost suppressed.

In old specimens the shape of the anterior parts of the notochord becomes rather irregular in section.

In that part of its course which lies behind the proboscis the notochord in the adult is more or less elliptical in section, containing a large and somewhat irregular lumen. Its tissue is here greatly reduced, and this reduction appears to progress regularly as the animal grows older. In fig. 60 the appearance of the notochord in such an old adult is shown. Degeneration has progressed far, leaving the notochord as a space surrounded by vacuolated cells enclosed in a sheath. With this sheath are connected the skeletal rods, which attain a great size. Centrally, on the dorsal side, between the notochord and the gut, lies the principal rod; this is formed by the uniting of the two rods (figs. 37, 38, &c.), whose development has already been described. This fused portion is now diamond-shaped in section; its lower angle causes a dorsal ridge to project into the mouth cavity. Laterally are placed two long rods, which are continued into the central rod and notochordal sheath anteriorly. To these lateral rods are attached large bunches of longitudinal muscles, by which, doubtless, the notochord may be pulled backwards, and the proboscis retracted so as to shut the mouth (fig. 60).

Posteriorly the median rod divides into two, and the opening from the notochordal lumen into the gut lies in the angle formed by the separation of these two diverging rods (fig. 57).

A considerable deposit of "structureless" substance takes place, filling up the spaces in the proboscis stalk, and forming a partial sheath around the perihæmal cavity. Whether this substance is chitinous or of some other material I am unable to say. The ensheathing parts of it have exactly the histological appearance presented by the "structureless" substance, which in *Amphioxus* is continued from the notochordal sheath,

&c., between the myotomes. The rods, however, are seen in adult specimens to have concentric markings in section, suggesting that they are formed by a deposit around a central core. In that part of the rod which lies just in front of the point of divergence of the two horns there are two such cores. The cores stain more deeply than the rest of the rods.

In *B. minutus* the position and general appearance of the notochord is similar to that in *B. Kowalevskii*, with the exception that the lateral rods are not developed to the same extent. The histology, however, is somewhat different. In figs. 61—63 the appearance of the tissue is shown. Spengel has stated that he is unable to find, in *B. minutus*, any structure resembling the notochord of the Chordata, figuring that organ as though composed of columnar cells. My own observations give no support to this statement. No specimen of notochord of any of the species which have been examined by me present the appearance indicated by Spengel. On the contrary, specimens preserved severally in picric acid, corrosive sublimate and acetic acid, Perenyi's fluid and osmic acid, all equally show this body as made up of vacuolated tissue strongly suggestive of the notochord of Chordata. This is especially the case with regard to that of *B. minutus*. Fig. 61 is taken from a section of *B. minutus* in front of the lumen. The sheath is here very slightly developed. It will be observed that the nuclei are fewer in number than in *B. Kowalevskii*, and that they are gathered round the upper centre. The section shown in fig. 62 is from the same in the region of the proboscis stalk. It shows the diamond-shaped section of the skeletal rod and the concentric markings upon it. The notochord itself is here elliptical in section, and the strands of protoplasm running across it are well seen.

Fig. 63 shows its appearance in front of the point at which it opens. Dorsally its wall is very thick and solid, while ventrally it is comparatively thin. Behind this part the skeletal rod divides into two divaricating horns as in *B. Kowalevskii*.

In the other species the structure of the notochord is

essentially the same as in *B. minutus*. In the anterior region of the notochord of *B. Brooksii* there are hardly any nuclei at all. I hope to publish figures illustrative of the later development and anatomy of the other parts at no distant date.

#### APPENDIX.

**Methods.**—From the characters of the unfertilized egg of *B. Kowalevskii* it was extremely improbable that the earliest stages of development could be passed anywhere else but in the mud which the parents inhabit. Though the examination of Agassiz had failed in the attempt to find any but adult *Balanoglossus* in this situation it seemed worth repeating. Accordingly a large quantity of mud inhabited by *Balanoglossus* was placed in a glass vessel of water and worked up, avoiding rotatory currents, until the whole was in suspension. A number of *Balanoglossus* which had previously been minced very finely were then thrown in and the whole was then left to settle for a few minutes. I then siphoned off the water and lighter particles in suspension, which consisted chiefly of vegetable *débris*, stopping the siphon when the layer of chopped *Balanoglossus* was reached, which could easily be seen by the bright orange colour of the fragments. This portion was drawn off and examined separately. It was found to contain great numbers of larvæ and embryos of *Balanoglossus*, minute Nemertines, free Nematodes, &c. In this manner all the animals living in several hundredweight of mud may, in an hour or two, be collected into about a pint of water and sorted with a simple microscope. This was generally performed by rotating a little of the water in a shallow saucer with a slight peripheral groove. The larvæ then all lie in the groove which may be passed under the lens by rotation. After a little practice it is of course unnecessary to discolour the water with fragments of the animal required, as of course the right layer can easily be detected by the size and character of the particles composing it. It appeared to be worth mentioning this mode of obtaining mud larvæ as its application on a large scale does not seem to be generally employed. It should be remarked that small

Nemertines, &c., are usually found still suspended long after most of the mud is precipitated. The water should then of course be poured off and left to settle separately. The degree to which any particular animals required may thus be easily separated off from the rest is very great. The disadvantage of such a method is that a certain number of larvæ are sure to be broken in the stirring necessary to effect suspension. I have little doubt that the larvæ which were observed free-swimming earlier than stage F were thus liberated from the egg-shell.

Preservation.—All my specimens of *B. minutus* were obtained from Naples, being very kindly prepared for me by Mr. Weldon with picric acid.

Most of the larvæ of *B. Kowalevskii* were placed for less than a minute in corrosive sublimate sat. sol. two parts, mixed with one part glacial acetic acid, washed with water and successively passed through 30 per cent., 50 per cent., 70 per cent., and 90 per cent. spirit. On the whole the results given by this reagent were the best. The softer parts, however, are best preserved in those specimens which were treated with Perenyi's fluid one hour, then 90 per cent. spirit for twelve hours, the 90 per cent. spirit being then changed. In the case of adults preserved with Perenyi's fluid, the fluid was changed once or twice.

Osmic acid did not give good results, but probably this was due to bad manipulation. The sections were cut in continuous series with Caldwell's automatic microtome.

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4. HATSCHKE, B.—"Stud. üb. Entw. d. *Amphioxus*," Claus's 'Arbeiten, Wien, 1881.
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## EXPLANATION OF PLATES IV—IX,

Illustrating the "Later Stages in the Development of  
Balanoglossus Kowalevskii, with a Suggestion as to  
the Affinities of the Enteropneusta."<sup>1</sup>

### *Complete List of Reference Letters.*

*a.* Anus. *Ac.* Archenteron. *Al.* Alimentary canal. *a. l.* Anal lappets. *bc.*<sup>1, 2, 3</sup>. The anterior, middle, and posterior body cavities respectively. The letters *l* and *r* affixed to these letterings denote that the parts are of the left or right side. *br.* Branchial chamber. *C.* Apical tuft of cilia. *C. N. S.* Central nervous system. *c. g.* Groove between the collar and the trunk. *cil.* Transverse band of cilia. *Cl.* Collar. *Cl'.* The posterior fold of the collar, which eventually forms the operculum. *Cl. sk.* Skin of collar. *D. b. v.* Dorsal blood-vessel. *D. mes.* Dorsal mesentery. *D. n. s.* Dorsal nervous system. *dig.* Digestive tract of alimentary canal. *E.* Ectoderm. *ex. g.* Refractive granules in mesoblastic cells. *f.* Mesoblastic fibres. *g. s.* Gill-slit. *g. s. r.* Branchial supporting rod. *gl.* Proboscis gland. *gl. s.* Sac of proboscis gland. *gn.* Ganglion (?) cells. *H.* Hypoblast. *ht.* Heart. *Int.* Intestine. *l. r.* Lateral rods of the skeleton. *lu.* Lumen of notochord. *M', M'', M'''.* Mesoblast derived from the anterior, middle, and posterior pouches respectively. *Mo.* Mouth. *msc.* Muscle-fibres. *mu.* Mucous gland. *n. s.* Nervous system. *cnl.* Neural canal. *Nc. pr.* Pore by which the notochord lumen opens into

the pharynx. *Nch.* Notochord. *N. pr.* Neural pore. *Op.* Operculum. *pkt.* Fibrous substance of the nervous system. *P. pr.* Proboscis pore. *P. h. b. c.* Perihæmal body cavity. *P. sk.* Skin of proboscis. *Sep.* Septum between the horns of the anterior body cavity. *Sh.* Sheath of notochord. *Skr.* Sucker. *Sk.* Skin. *S. r.* Supporting rod. *Sk.* Skin. *Sp.* Tissue-space in the proboscis cavity. *ts.* Testis. *V. vs.* Ventral vessel. *V. n. s.* Ventral nervous system. *Vlv.* Valve of gill-slit. *x.* Pyriform cells of splanchnopleure of middle body cavity.

With the exception of Figs. 5 and 6, the outlines were all drawn with Zeiss's camera lucida. I have to thank Mr. Edwin Wilson of the Lithographic Department of the Cambridge Scientific Instrument Company for drawing for me two beautiful figures (Figs. 5 and 6) of the whole animal from preserved specimens, and also for Figs. 1, 2, 3, and 4, which he has prepared for me from my own sketches, the original outlines of which were traced from living specimens.

FIG. 1.—Whole animal seen from the side, immediately after the appearance of the second pair of gill-slits. (Obj. A, oc. 2.)

FIG. 2.—Similar view of an older animal, with two gill-slits. (Obj. A, oc. 2.)

FIG. 3.—Similar view of a three-gill-slit larva. (Obj. A, oc. 2.)

FIG. 3a.—Posterior end of the same in a retracted state, seen in profile (from a preserved specimen). (Obj. A, oc. 2.)

FIG. 4.—Side view of larva with five pairs of gill-slits. The fold of the operculum covering part of the first gill-slit is semi-transparent. (Obj. A, oc. 2.)

FIG. 5.—Side view of preserved specimen with nine pairs of gill-slits. Owing to the contraction of the body and the protrusion of some of the valves, few only of these are visible. (Obj. AA, oc. 2.)

FIG. 6.—The adult animal (♂). ( $\times 2$  diameters.)

FIG. 7.—Longitudinal vertical section (not quite median) of a larva in Stage F. (Obj. C, oc. 2.)

FIG. 8.—Cells of mesoblast of anterior pouch, from a transverse section of a larva shortly after this pouch is closed off from the hypoblast. (Obj. F, oc. 2.)

FIG. 9.—The same tissue from the posterior third of the proboscis of a rather older larva, showing the proliferation and commencing differentiation of the mesoblastic elements. (Obj. D, oc. 2.)

FIG. 10.—Section similar to Fig. 7, from a rather older larva to show anterior, dorsal structures (Stage G—H). (Obj. D, oc. 2.)

Figs. 11—20 represent transverse sections of a larva in Stage G—H, with the exception of Figs. 12 and 16, which were drawn under Obj. F, oc. 2. All these figures were drawn under Obj. CC, oc. 2. In most of these figures the ectoderm is only indicated on a short arc of the circle of the whole section. They are numbered from before backwards.

FIG. 11.—Transverse section of proboscis cavity. Mesoblastic elements distributed nearly uniformly all round the interior.

FIG. 12.—Portion of these mesoblastic elements more highly magnified, to exhibit the differentiations.

FIG. 13.—Section taken behind Fig. 11. The mesoblastic layer is thinner dorsally than elsewhere.

FIG. 14.—In this section the septum separating the two horns of the cavity is reached.

FIG. 15.—Still further back the first rudiment of the proboscis gland is reached (cp. Fig. 29).

FIG. 16.—The rudiment of the gland lying in the septum more highly magnified.

FIG. 17.—Section across the proboscis stalk. The anterior end of the notochord is reached. The back of the gland is nearly passed. The mesoblastic horn of the left side is apparently divided into two parts, this appearance is due to shrinking.

FIG. 18.—The lumen of the notochord is reached. The extreme ends of the two anterior mesoblastic horns and the posterior apex of the left horn from the first cavity are all cut in this section. (The irregular folds of skin are due to the contractions of the body; it will be understood by comparing the figures of the whole animal that only the central part within the folds is the real stalk of the proboscis.)

FIG. 19.—The section crosses the end of the archenteron, lying in front of the mouth. (The whole of this part of the archenteron becomes eventually pushed forward to form the notochord.)

FIG. 20.—The mouth is here traversed, as also the anterior end of the nervous system. (A space, due probably to shrinking, is visible in the dorsal mesentery.)

Figs. 21—29 are transverse sections of a larva, slightly older than the foregoing. Fig. 25 was drawn under Zeiss's Immersion 2 and oc. 2; the others were drawn under Obj. D and oc. 2. They are numbered from before backwards.

FIG. 21.—Section taken just behind the mouth. The lumen of the notochord is here shut off from the archenteron.

FIG. 22.—The notochord still open to the archenteron.

FIG. 23.—The nervous system is attached to the skin.

FIG. 24.—The nervous system is already nearly separated from the skin.

FIG. 25.—Part of the foregoing enlarged, to show the peculiar pyriform cells of the splanchnopleure (*x*).

FIG. 26.—Nervous system still in the skin.

FIG. 27.—The nerve-cord is separated from the skin.

FIG. 28.—Two parts of the middle body cavities may be here seen separating from the rest, probably forming part of the perihæmal cavities.

FIG. 29.—The anterior ends of the third pair of body cavities are here cut as a solid mass of mesoblast on each side.

FIG. 30.—A longitudinal vertical, nearly median, section of a larva, in the same stage as that shown in Figs. 21—29. The differentiation of the walls of the digestive tract may be here seen.

Figs. 31—44 are from transverse sections of a larva which has just acquired the second pair of gill-slits. They are numbered from before backwards.

FIG. 31.—Transverse section of the proboscis cavity. The loose tissue in the sac of the gland is shown. The membrane which is deposited round it is visible (cp. Fig. 47). (Obj. D, oc. 2.)

FIG. 32.—Small portion of skin and mesoblast on a larger scale, to show structure of the nervous layer. (Obj. F, oc. 2.)

FIG. 33.—Region behind that shown in Fig. 31. (Obj. D, oc. 2.)

FIG. 34.—Through the proboscis stalk. The anterior horns of the middle body cavities are here cut.

FIG. 35.—Through the proboscis stalk and the anterior phlange of the collar which forms the lower lip.

FIG. 36.—Through the anterior end of the nervous system (in the region of the mouth), showing the manner in which the lumen arises in the nerve-cord.

FIG. 37.—Through the anterior part of the collar, showing the nearly complete separation of the notochord with the hypoblast.

FIG. 38.—Section taken behind the previous one. The nervous system is here separated from the skin.

FIG. 39. Through the junction of the lumen of the notochord with that of the gut. The skeletal rods, which here bend downwards, backwards, and then slightly forwards, are therefore cut twice on each side.

FIG. 40 is taken rather in front of the branchial sacs; it shows the two anterior horns of the posterior body cavities, which form the perihæmal cavities.

FIG. 41.—Section through the gill-sacs in front of the clefts. The nervous system here is fused to the skin dorsally.

FIG. 42.—Through the extreme posterior end of the second body cavities, and the anterior end of the ventral blood-vessel and nervous cord.

FIG. 43.—(Section not quite transverse.) Through the left gill-slit.

FIG. 44.—Section taken through the extreme posterior end of the branchial region of the gut, showing how this overlaps the digestive region. The dilatation in the sides of the branchial region here shown are parts of the second pair of gill-slits.

FIG. 45.—A longitudinal vertical section of the whole animal. (Two gill-



slits.) (The section is not truly vertical, as it cuts the gill-slit.) It exhibits the relation of the notochord and other parts. (Obj. CC, oc. 2.)

FIG. 46.—By an oversight no figure bearing this number appears in the plates. The figure referred to as such in the text at pages 85, 98, and 103, is Fig. 45.

FIG. 47.—A transverse section of the extreme tip of the notochord, &c., in the larva from which Figs. 31—45 were taken. It shows the histology of the notochord and the arrangement upon it of the mesoblastic tissues, which are pushed in by it. (Obj. D, oc. 2.)

FIG. 48.—Transverse section across the proboscis pore of a larva with three gill-slits. The two skeletal rods are here fused and have attained a considerable size. (Obj. F, oc. 2.)

Figs. 49—53 represent transverse sections taken from *B. Kowalevskii*, at the stage of four pairs of gill-slits. (When the remaining structures are dealt with a fuller explanation will be given of these and of the subsequent figures; on the present occasion they are only introduced to explain the account of the notochord given in the text.) Figs. 49—53 are numbered from before backwards.

Figs. 49 and 50 illustrate the histology of the anterior end of the notochord. (Obj. F, oc. 2.) These sections are in front of the heart.

FIG. 51 shows a section of the whole proboscis, to illustrate the relations of the parts. The body cavity may be seen to be nearly filled up with muscle-fibres and connective tissue, with the exception of a small central space, in which lies the notochord bearing the central mesoblastic structures, viz. the heart and proboscis gland with its sac. (Obj. C, oc. 2.)

FIG. 52 exhibits the central structures of Fig. 51. (Obj. F, oc. 2.)

FIG. 53.—Here the lumen of the notochord is reached. At this point the sac of the proboscis gland is attached dorsally to the skin of the proboscis. (Obj. F, oc. 2.)

FIG. 54.—Transverse section of proboscis stalk of an older animal, taken behind the epiblast sac of the proboscis pore, the back of which appears in section. The skeletal rod has still in this region two central "cores." (Obj. D, oc. 2.)

FIG. 55.—A transverse section of the notochord of an adult *B. Kowalevskii*, taken in front of its lumen (cp. Fig. 57). (Obj. CC, oc. 2.)

FIG. 56.—Transverse section of the same as foregoing, through the dilated lumen in front of the skeletal rod.

FIG. 57.—Longitudinal vertical median section of the back of the proboscis and the front of the collar of *B. Kowalevskii*, to show the relation of the notochord. The other parts are diagrammatic. (Obj. A, oc. 2.)

FIG. 58.—Transverse section of the junction of the proboscis stalk with the collar. (Semi-diagrammatic.) Exhibits relations of the notochord and its sheath to the skeletal rods, nervous system, &c. (Obj. A, oc. 2.)

FIG. 59.—A diagram of a transverse section taken through the anterior region of the collar, to show the relation of the parts figured in Fig. 60. (Obj. A, oc. 2.)

FIG. 60.—The dorsal structures of the anterior part of the collar shown in Fig. 59, viz. the nervous system, notochord, perihæmal cavities, &c. (The gut is torn away from the skeletal rod, presumably by shrinking.) The lateral rods are here connected to the notochordal sheath. (Obj. D, oc. 2.)

Figs. 61—63 show transverse sections of parts of *B. minutus*.

FIG. 61.—The notochord in transverse section in front of its lumen. (Obj. CC, oc. 2.)

FIG. 62.—The same in the region of the proboscis stalk.

FIG. 63.—Through the notochord, &c., in the front of the collar, showing the thickened dorsal half of the organ. (Obj. CC, oc. 2.)

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#### ERRATUM.

In the body of the preceding paper (not in the Description of the Plates), for Fig. 45, read Fig. 44, and for Fig. 46, read Fig. 45.

## Some Notes on the Early Development of *Rana temporaria*.

By

**W. Baldwin Spencer, B.A.,**  
Scholar of Exeter College, Oxford.

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With Plate X.

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THE following work has been carried on chiefly in the laboratory of the University Museum, Oxford; and I must here acknowledge the kindness and assistance received from Professor Moseley.

This paper deals firstly with the question of the fate of the blastopore, and secondly with some points in connection with the early development of the cranial nerves. I hope before long to publish a further paper dealing with the latter subject.

### (1) FATE OF THE BLASTOPORE.

Up to very recent times it was stated, in accordance with the well-known investigations of Götte on Bombinator and Scott and Osborne on Triton, that in both anurous and urodelous Amphibians, the blastopore was enclosed by the growth of the neural<sup>1</sup> folds, and thus formed a means of communication

<sup>1</sup> Would it not be much simpler, if instead of using the term "medullary" in connection with the development of the central nervous system, the word "neural" were used throughout? We should then have a complete, uniform series of terms, viz. neural plate, neural folds, neural groove, neural canal, neural ridge, and also neurenteric canal. In this article I have adopted the above nomenclature.

between the neural and alimentary canals, whilst the anus was subsequently formed as a proctodæum.

Miss Johnson,<sup>1</sup> however, has shown that the neural folds do not thus enclose the blastopore in Triton, but that in this form it remains open and forms the permanent anus.

Some little time previously Oskar Schulze published an account of his investigations with regard to the early development of Batrachians, and his paper is accompanied by a careful series of drawings, which, however, consist exclusively (save one small diagrammatic section) of external views of *Rana fusca*.

He states<sup>2</sup> that the blastopore closes up, and that the anus is formed as a proctodæum very closely behind the posterior end of the neural folds.

As before said, however, he figures no sections, and more lately an investigation of the egg of *Rana temporaria*, both by means of external views and of numerous series of consecutive sections, has given me a very different result, and one which differs also in important details from that described by Miss Johnson for Triton.

The neural folds, as is well known, stretch back on the dorsal surface as far as the blastopore, and though but very slightly raised in this part they appear to pass round and join each other behind, as seen in figs. 2 and 3.

Figs. 1, 2, and 3 show different stages during the growth of the folds, and in the last of these they are seen to have met, though the line of union is distinctly marked, and—most important—the blastopore is not enclosed.

So far the account agrees with that of Götte for Bombinator, the figures from which are copied in Balfour's 'Embryology.' When this stage has been reached, however, according to Götte, and after the blastopore has remained open to the exterior for some little time, the neural folds continue to grow and enclose it, whilst still later a proctodæum is formed some distance anterior to this upon the ventral surface.

<sup>1</sup> 'Quart. Journ. Mic. Sci.,' Oct., 1884.

<sup>2</sup> 'Archiv. für Mikr. Anat.,' Oct., 1883, part i.



I have, however, in *Rana*, been unable to find any trace of this closure, and in fig. 4 is given a view of the ventral surface of an older embryo, in which the tail is just beginning to grow out, and the line of union of the folds is but faintly marked, whilst at the end of the latter, and occupying the same position as in figs. 2 and 3, is yet the blastopore.

At this stage the line of union may or may not be traceable, but the aperture retains the same relative position, and as growth proceeds remains open, and can be traced through still older specimens until the adult stage is reached.

This gradual transformation is shown by external views in figs. 1—4, whilst it is fully confirmed by the series of sections in figs. 5—15.

Figs. 5, 6, and 7 represent transverse sections through an embryo of the age shown in fig. 1, whose neural folds are yet open.

Fig. 7 is the most anterior section, and shows the open neural groove on the dorsal surface, while the alimentary canal is cut in section in the middle of the yolk.

Fig. 6 represents a more posterior section through the neural groove dorsally and the blastopore ventrally, while in fig. 5 the two folds are cut through as they pass round the posterior end of the egg. (The section is oblique, and hence more is cut through on one side than the other.) The sections show that the neural groove runs right back to the blastopore.

Figs. 8—11 are from similar sections of an older embryo (such as fig. 3 represents), whose neural folds have met, their line of union being seen in the most posterior section (8), while one (9), just anterior to this, cuts through the posterior part of the neural canal which runs round the hinder part of the egg to open at the blastopore. Owing to the direction in which it runs a transverse section, such as is represented in fig. 9, cuts through a considerable part of its length.

The two anterior sections show the neural canal dorsally and the alimentary canal ventrad of this.

After this stage has been reached a further important development takes place; the hinder part of the neural canal,

which opens into the blastopore, becomes closed though the blastopore itself remains open. This apparently is caused by growth of the epiblast cells lining the neural canal, and, inasmuch as they contain much pigment, the position of the former canal, connecting the neural and alimentary canals, is plainly indicated by a line of dark cells seen well in section.

Figs. 12—14 represent transverse sections through an embryo of the age of fig. 4, in which the primitive blastopore still opens into the alimentary canal, but yet no open connection exists between this and the neural canal, which posteriorly ends in a solid cord of cells. At this period, as is well seen in fig. 15, which represents a longitudinal vertical section of an embryo, there is, at the posterior end around the blastopore, a fusion of the different cell layers. Into this fused mass appear to enter the cells of the external epiblast, of the neural canal, of the notochord, of the hypoblast of the alimentary canal, and of the yolk, whilst at a slight distance anteriorly the mesoblast grows out of this.

Thus both sections and external views lead to the same conclusion, that in *Rana*, as in *Triton*, the blastopore is transformed into the permanent anus, though there is the not unimportant difference between the two, that in *Triton* no connection exists between the neural and alimentary canals, whilst such a structure is well marked in *Rana*.

Balfour<sup>1</sup> (after Götte) figures a longitudinal section of *Bombinator* at a stage considerably after the neural folds have met and fused, and when, according to this older theory, the blastopore has been enclosed and a neurenteric canal formed. The same section shows the formation of a proctodæum, and the presence of a so-called post-anal gut. In no section out of the numerous series cut have either of these structures been seen in *Rana*, and yet, inasmuch as, by means of dorsal growth, the blastopore is carried round the posterior end till it lies some little distance anteriorly on the ventral side, there is a time at which the hinder end of the neural canal opening into the blastopore occupies exactly the position of the post-anal

<sup>1</sup> 'Comp. Embryolog.,' vol. ii, p. 107.

gut of Götte: not only is this the case, but the blastopore also is situated in precisely the same position in which, according to him, the proctodæum is being formed.

May it not thus be possible that what Götte calls the post-anal gut, and which, according to him, closes up after formation of the proctodæum, is in reality the posterior part of the neural canal which in early stages opened into the blastopore, but which, later on, disappeared?

It is further rather difficult perhaps to say whether, strictly speaking, a neurenteric canal is present in *Rana*, as this term is usually used in connection with the enclosure of the blastopore, and when this itself forms a means of communication between the alimentary and neural canal. Perhaps, however, the term "neurenteric canal" may be applied to all structures which allow of communication between the two canals, and which itself, in subsequent development, closes up and disappears: using the term in this sense one is clearly present and well developed in *Rana*.

## (2) SOME POINTS CONNECTED WITH THE EARLY DEVELOPMENT OF THE CRANIAL NERVES.

The following are a few notes connected with the early development of the cranial nerves of the Amphibia, and I must acknowledge my indebtedness to Professor Marshall for kind assistance, and for his permission to use the laboratory and materials of the Owens College.

Sections of eggs of *Rana* as early as the close of segmentation show that the epiblast is formed of two distinct layers of cells, the outer of which is one cell deep, whilst the inner varies much in thickness in different parts and continues to do so during development.

Of these the first is the epidermic and the second the nervous layer, and the development of the whole of the nervous system, save the lining of the neural canal, is concerned solely with the latter.

On what will ultimately be the dorsal surface of the embryo

is formed the neural plate by a great proliferation of cells in the nervous layer; this plate becomes first of all grooved longitudinally by the primitive groove, and then in the well-known way the neural folds grow up dorsally, enclose the neural groove, and finally, after meeting each other, the neural canal.

During this course of development the greatly thickened neural plate as it becomes transformed into the walls of the neural canal retains its primitive connection with the nervous layer of the epidermis as is well shown in figs. 7, 11, 16, &c.; in the first of these the neural folds have not yet fused dorsally and the groove is wide open.

The axolotl differs, however, in one respect from the frog, agreeing with the newt in having at first the epidermis of one cell thick, though after closure of the neural folds the two layers appear, and further development seems to be similar to that of *Rana*.

This inner nervous layer is intimately connected with the development not only of the central nervous system, but also with that of the sense organs of the body, the auditory sac, the olfactory organ, the sense organs of the lateral line, and, most important of all, it is, as I hope to show, intimately related to the formation of the peripheral nervous system.

Without taking the latter into account at the present moment there may be said to exist in the Amphibian embryo a complete superficially placed nervous sheath out of which not only the central nervous system, but all the sense organs of both head and trunk are formed and which gradually disappears as these reach their full development.

The following notes refer to the origin of the cranial nerves, and I hope shortly to publish a complete account of these and of the spinal nerves. Owing to the great difficulty in distinguishing the cells of the various germinal layers at early stages it is no easy matter to ascertain the manner in which the nerves develop and in the sections figured the mesoblast has been omitted for the sake of clearness.

Before the closure of the neural canal no development of



nerves can be perceived ; there is simply the nervous sheath of the epiblast surrounding the whole body and connected with the lateral edge of the neural plate, and as this gradually bends up on each side, with the dorsal lips of the neural groove (fig. 7), and finally, with the dorsal surface of the neural canal (figs. 11 and 14).

In the chick<sup>1</sup> before closure of the neural canal a neural ridge is present on each side of the brain, and from this as outgrowths the nerves are formed ; in Elasmobranchs,<sup>2</sup> though developed somewhat later, a well-marked neural ridge is present and the origin of the peripheral nervous system apparently corresponds closely with that of the chick, but in Amphibia I have been unable to discover any such structure as a neural ridge, and it is only when the neural folds have met and fused completely, and the neural canal quite separated off from the epidermic layer that the earliest rudiments of nerve appears.

This earliest appearance does not assume the form of a direct outgrowth from the substance of the neural canal, but a series of consecutive transverse sections shows that along certain lines the cells of the nervous layer proliferate, and it is by this proliferation that the rudiments of the cranial nerves are laid down.

This is most clearly seen in the case of the trigeminal and facial nerve, and figs. 16—20 represent stages in the development of the former nerve.

In fig. 16, on the left side, the nervous layer of the epidermis is seen to have proliferated (for, save at the part where nerves are formed and along the lateral line, it is only one cell thick on the sides of the embryo), and it is seen further that this proliferation extends for almost the whole length of the side.

The section is an oblique one so that one side passes through the optic vesicle, and here the nervous layer is only one cell thick except where at the level of the lateral line the very front part giving rise to the Gasserian ganglion is cut through.

<sup>1</sup> Marshall, 'Quart. Journ. Mic. Sci.,' vol. xviii, 1878.

<sup>2</sup> Balfour, 'Monograph on Elasmobranch Fishes,' London, 1878.

Section 19, which is taken from an axolotl, shows the same proliferation, and also that this is greatest at the level of the lateral line. In course of development the string of cells thus formed becomes gradually separated off from the nervous layer of the epidermis, which retains its normal thickness of one cell and for some time afterwards the exact boundary of the nerve is ill-defined, while the mesoblast grows in between it and the epiblast, the only point at which it remains connected with the latter being that at which the Gasserian ganglion is developed.

This is seen in section 17, where the main strand of the trigeminal is seen separated from the epiblast, while in fig. 18, a slightly more anterior section, the Gasserian ganglion is yet connected with the epiblast; in fig. 17 the nerve should be represented as lying somewhat nearer to the surface.

In further development the whole nerve and ganglion comes to lie within the mesoblast, and, as seen in fig. 20, the latter quite loses its connection with the epiblast.

This development of the ganglia at the level of the lateral line, and the fact of their long connection with the epiblast at this point, when all the rest of the nerve has been separated off, is of great interest in connection with certain points in the development of the Elasmobranch nerves to be shortly noticed.

With regard to the development of roots, I hope to be able soon to publish some detailed account. At the earliest period at which they can be recognised they appear to arise from the dorsal summit of the brain, and, as shown in figs. 16 and 19, to originate by proliferation from the nervous layer, which afterwards separates entirely from the brain, and can be traced running right across the head dorsally.

In the region of the trunk, a considerable period after the cranial nerves are well formed and recognisable, there seems to be no development of spinal nerves, though the nervous sheath is clearly developed, and in this the lateral line.

Through the kindness of Dr. Beard I have been enabled to examine several beautiful series of sections of Elasmobranch embryos, and he has also allowed me to introduce into this

article one or two points of interest derived from the study of them, and which are of some importance in connection with the development of the cranial nerves.

They are, moreover, conclusions at which Dr. Beard has himself also arrived.

Fig. 21 represents a transverse section through the head of an Elasmobranch embryo, and, owing to cranial flexure, the three divisions of the brain are all cut through. Arising from the dorsal surface of the hind brain may be seen the two rudiments which will give rise in development to the trigeminal nerve. These arise apparently quite independently of the epiblast, with which, at this early stage, they have no connection, but are connected solely with the nervous matter of the neural canal.

Figs. 22, 23, and 24, however, are similar sections through the head of a somewhat older embryo, the first-mentioned being the most anterior section, and the other two being cut at slight intervals posterior to this. In these three is seen part of the course of the trigeminal nerve, which at one point has become clearly fused with the epiblast. It is at this point, after the fusion has taken place, that the Gasserian ganglion is formed.

In the sections the cells of the epiblast at this point seem to have undergone considerable proliferation, and an examination leads to the conclusion that the Gasserian ganglion is, at all events in part, formed directly from the epiblast.

The importance of this origin and relation to the epiblast of the Gasserian ganglion, and the fact that the same development takes place in the case of the ganglia of the third and seventh nerves—in that of the ciliary ganglion the development is particularly clear—becomes still more important when taken in connection with the particular part of the epiblast with which the ganglia are so intimately connected in early stages.

The ganglia arise along the level of the lateral line continued on to the head.

Professor Marshall has previously described<sup>1</sup> the ciliary and

<sup>1</sup> "On the Head Cavities and associated Nerves of Elasmobranchs,"

Gasserian ganglia as arising from the first as swellings of the third and fifth nerves respectively, which are, from the earliest time of their appearance, hemmed in between the first and second and second and third head cavities. This description must now be modified, as primitively these ganglia arise in immediate connection with the epiblast, and only come to occupy their previously-described position at a later stage of development.

This curious origin of the ganglia of the cranial nerves points strongly to the conclusion that primitively they arose as ganglia of the sense organs of the lateral line in the head, and that their present position and nature must therefore be regarded as a secondary, and certainly not primitive, condition.

In passing, I may just notice that on this supposition an explanation is offered as to the origin and meaning of the two curious branches<sup>1</sup> which unite respectively the ganglia of the fifth and seventh and fifth and third cranial nerves; they may be regarded as the persistent parts of the lateral nerve which united the ganglia of the sense organs along the lateral line in the head, and which, separating from the skin, have come in the course of development to occupy a much deeper position, together with the ganglia, with which they preserve their primitive connection.

The development (though taking place, partly at all events, directly from the epiblast) of the ganglia and nerves above given, varies considerably and in very important points from that given by His for the chick.

According to this investigator<sup>2</sup> the ganglia are developed from an "intermediate cord" (Zwischenstrang), which is developed out of the floor of an "intermediate groove" (Zwischenrinne), which is itself derived from the epiblast, and not from the neural folds whilst these are closing over.

<sup>1</sup> 'Quart. Journ. Mic. Sci.,' Jan. 1, 1881; also Marshall and Spencer, "Observations on Cranial Nerves of Scyllium," 'Quart. Journ. Mic. Sci.,' July, 1881.

<sup>2</sup> See Marshall and Spencer, *op. cit.*, July, 1881, fig. 10, *Nc'* and *Nc*.

<sup>3</sup> 'Arch. für Anat. und Phys.,' 1879.



The position of this "Zwischenstrang" varies in different parts of the body and in the head where it lies between the neural canal and the epiblast; after uniting with the central nervous system<sup>1</sup> it gives origin to the Gasserian, auditory, glosso-pharyngeal, and vagus ganglia.

This origin hence differs essentially from that given above in Elasmobranchs, where the nerve first grows out of the brain (i. e. from the neural ridge), and only subsequently fuses with the epiblast where the ganglia are formed, and, moreover, this fusion takes place at a very different level from that described by His as occurring in the chick, and shown by him<sup>2</sup> also in the section which he figures of Scyllium. He also draws two sections of frog embryos, and marks on them the position of the "Zwischenrinne," but his figures do not show the very clear double nature of the epiblast, and it is to this that is due the method of development of the peripheral nervous system above described.

It is possible that the condition which obtains in the Amphibia<sup>3</sup> may be an exceedingly primitive one. The possession of what must be regarded as a complete nervous sheath points in this direction, and the development in such forms as the chick and Elasmobranch, where the epiblast does not separate into its two constituent parts, may be regarded as a considerably modified one. It is important to notice also in this connection that, where in Elasmobranchs the nervous layer of the epidermis may be regarded as most developed—that is about the level of the lateral line—the cranial nerves here fuse with the epiblast, and at the point of fusion the ganglia are produced.

Possibly the neural ridge which grows out from the central nervous system may be taken as representing, in a highly-modified form, the nervous layer which in Amphibians sur-

<sup>1</sup> Op. cit., figs. iii, *a*—*f*.

<sup>2</sup> Op. cit., fig. xi, *z*.

<sup>3</sup> It is exceedingly likely that in Teleostei and Lepidosteus where the epiblast is also double, that the peripheral nervous system will be found to originate in the same way.

rounds the whole body. In Elasmobranchs the whole epiblast does not divide into two layers, and hence the nerves must be developed in some different way. After formation of the neural canal the nervous matter of its walls grows very rapidly, and gives off on each side the neural ridge, from which as lateral outgrowths the nerves are formed by cell proliferation, the parts of the ridge not used in development of the nerves disappearing, just as in the Amphibia, after formation of the nerves and sense organs, the remainder of the nervous layer gradually atrophies, and finally disappears as a distinct structure.

This will, at all events, explain the fact of there being a continuous neural ridge along the dorsal surface of the central nervous system, the intermediate parts of which disappear after formation of the nerves.

The proliferation of nerves in Amphibia shows a remarkable resemblance to that of the lateral and pedal nerve-cords which has recently been described by Kowalevsky as occurring in Chiton.<sup>1</sup> Fig. 25 is copied from one of his figures (fig. 60) and shows the thick epiblast on the ventral surface giving rise by simple proliferation to the nerves, and when compared with figs. 16 and 19 of Amphibian sections the process will be seen to be an essentially similar one in the two cases.

It is interesting further to observe that a neural sheath is actually found existing throughout life in some of the invertebrates, in which sheath greater or less differentiation for the formation of nerves takes place.

Thus in some Cœlenterates a rudimentary and ill-defined sheath may be present; in the schizo- and palæo-Nemertines one is well developed and in the latter lies close to the epiblast, whilst long lateral nerve-cords are developed from the sheath, though they retain their connection throughout life, while finally, Professor Marshall has suggested that the Echinodermata may be supposed to have had a nerve-sheath immediately below the epidermis surrounding the whole body, and out of which both the nerve-cords of crinoids may be formed, the

<sup>1</sup> Mémoire No. 5, 'Annales du Muséum Histoire Naturelle de Marseille,' "Embryogénie du Chiton Polii."

dorsal one having been separated off whilst the ventral still retains its primitive connection with the persistent neural sheath.

The Amphibian embryonic neural sheath may possibly hence represent a primitive condition, and the formation from it of sense organs and nerves, resembling as it does that which is found in certain Invertebrates, may reveal a more ancestral process than the method of their formation in Elasmobranchs and birds.

## DESCRIPTION OF PLATE X,

Illustrating Mr. W. B. Spencer's Paper on "Some Notes on the Early Development of *Rana temporaria*."

### *Alphabetical List of References.*

*al.* Alimentary canal. *an.* Anus. *bl.* blastopore. *ep.* Epiblast. *ep'.* Epidermic layer. *ep''.* Nervous layer. *f. b.* Fore brain. *gass.* Gasserian ganglion. *h. b.* Hind brain. *hy.* Hypoblast. *lat.* Lateral line. *mes.* Mesoblast. *n.* Pedal nerve. *n'.* Lateral nerve. *n. c.* Neural canal. *n. f.* Neural folds. *n. g.* Neural groove. *n. r.* Neural ridge. *ne. c.* Neurenteric canal. *no.* Notochord. *olf.* Olfactory organ. *op. v.* Optic vesicle. *sc.* Suckers present in embryo frog. *yk.* Yolk. *2.* Second head cavity. *V.* Trigeminal nerve. *x.* Point of fusion of layers.

FIGS. 1—4 represent external views of embryos of *Rana temporaria*.

Fig. 1.—From the dorsal surface. The neural folds have not yet closed, and are especially wide open in the head region.

Fig. 2.—The posterior end of an older embryo, seen from the ventral surface. The folds are just meeting, but not obliterating the blastopore.

Fig. 3.—A similar view of a slightly older embryo. The folds are still closer, but the blastopore persists.

Fig. 4.—Ventral view of a considerably older embryo, in which the tail is just beginning to grow and the line of union of the folds is but very faintly marked, the blastopore persisting as the anus at its end.

FIGS. 5—7 represent transverse sections through an embryo of the age of Fig. 1 in the posterior region.

Fig. 5.—The most posterior section and cut somewhat obliquely through the medullary folds, showing the groove between these running to the blastopore.

Fig. 6.—Cuts through the blastopore below and the open neural groove above.

Fig. 7.—A more anterior section shows the groove still open above, and the alimentary canal lying in the midst of the yolk-cells. The nervous layer is seen continuous round the body, and connected with that portion which has become much enlarged to form the neural folds.

FIGS. 8—11.—Transverse sections through an embryo intermediate in age between those in Figs. 3 and 4. The folds have closed over and the neural canal opens into the blastopore.

Fig. 8.—The most external and posterior section shows the line of union of the folds.

Fig. 9.—Cuts through the part of the neural canal which opens into the blastopore.

Figs. 10 and 11 are more anterior sections and show the alimentary canal and neural canal cut in sections, fig. 10 passing through the blastopore below.

FIGS. 12—14 represents sections through an embryo of the age of Fig. 4.

Fig. 12.—Most posterior section passing through the blastopore.

Fig. 13.—More anterior section, showing the alimentary canal into which the blastopore has opened below, and a line of dark cells leading up to the dorsal surface where the neural canal is seen dimly outlined. The dark cells represent the open passage of Fig. 9.

Fig. 14 represents a more anterior section of the same embryo.

FIG. 15.—A vertical longitudinal section through an embryo of the same age as in Fig. 4. The fused layers are seen at *x*, and the hinder part of the nervous system is solid and has lost its opening into *an.*, which corresponds to the blastopore which has not closed up.

FIG. 16.—Transverse section through an embryo of *Rana temporaria*, showing proliferation of the cells of the inner nervous layer of the epidermis to form the fifth cranial nerve. On the right side the Gasserian ganglion is seen in course of formation.

FIGS. 17 and 18.—Transverse sections through a somewhat older embryo to show the position of the fifth nerve after separation from the epiblast, except at the point where the Gasserian ganglion is formed.

FIG. 19.—Transverse section through an axolotl embryo, showing the formation of the fifth nerve on each side.

FIG. 20.—Transverse section through a much older embryo of *Rana*



temporaria, to show the complete separation of the Gasserian ganglia from the epiblast.

FIG. 21.—Transverse section through the head of an Elasmobranch embryo, to show the early origin of the fifth nerve.

FIGS. 22—24.—Transverse section through the head of a somewhat older embryo, to show the fusion of the fifth nerve with the epiblast and the formation at this point of the Gasserian ganglion.

The Figs. 21—24 are drawn from sections kindly lent to me by Dr. Beard.

FIG. 25.—From Kowalevsky. Transverse section through a developing *Chiton polii*, to show the formation of the nerve-cords by proliferation.



## Notes on Echinoderm Morphology, No. IX. On the Vascular System of the Urchins.

By

**P. Herbert Carpenter, D.Sc.,**

Assistant Master at Eton College.

EIGHTEEN months ago I published a note in this Journal,<sup>1</sup> which contained a partial analysis of the excellent memoir by Koehler upon the minute anatomy of the Echinoidea.<sup>2</sup> I was led more particularly to discuss those of his observations which dealt with the vascular system, and their bearing upon the two theories as to its anatomical relations which are current among morphologists. Many of these observations go far to support the views of Ludwig respecting the general morphology of the Echinoderm vascular system; while others seem as decidedly opposed to them, and in favour of Perrier's theory as to the fundamental unity of the double vascular system of an Echinoderm, and the communication of the so-called "heart" with the exterior through the pores of the madreporite.

At the same time I ventured to notice what appeared to me to be certain weak points in Koehler's chain of evidence—points which it was desirable to have thoroughly established, as being those on which the theory of Perrier and Koehler mainly rested.

If the French zoologists are in the right we must either

<sup>1</sup> "Notes on Echinoderm Morphology, No. VI. On the Anatomical Relations of the Vascular System," 'Quart. Journ. Micr. Sci.,' vol. xxiii, 1883, pp. 597—616.

<sup>2</sup> "Recherches sur les Echinides des Côtes de Provence," 'Ann. du Mus. d'Hist. Nat. de Marseille, Zoologie,' Mémoire No. 3, pp. 1—167, pl. i—vii, 1883.

admit that the results of their German colleagues, and more especially those of Ludwig, are in many respects very incorrect; or else that the vascular system of an Urchin is far more different from that of a Starfish than has been hitherto supposed.

The zoological group Echinodermata is so extremely well defined, and has so few direct relations with other classes of animals, that we are justified in expecting a close correspondence in fundamental characters among the different members of the group. Readers of this Journal will not need to be reminded of the detailed homologies which have been recently demonstrated in the Apical Systems of the three classes of Brachiate Echinoderms. The same may be said of the nervous system throughout all the Echinodermata, and, as I fully believe, of the vascular system too. But where one author tells us that the oral blood-vascular ring of a Starfish is in direct communication with an elaborate system of genital and visceral vessels beneath the dorsal surface, while another asserts that the corresponding structure in an Urchin communicates with the exterior through the madreporite, it is difficult to avoid the suspicion that further observations, conducted by the same method in both cases, may reveal an error somewhere.

In the note to which I have referred allusion was made to a few points of this nature, in the hope that the authors concerned might take up the question again, so as to bring out more clearly the points of agreement or difference between them.

Stimulated by my criticisms of what I, rightly or wrongly, conceived to be certain possibilities of error in Koehler's treatment of his subject, he has returned to it again with the following results<sup>1</sup>:—"Quoiqu'il en soit de cette discussion, je ne puis que maintenir les résultats auxquels je suis arrivé. J'ai répété mes injections un assez grand nombre de fois voulant vérifier les faits que j'avais, surtout au sujet des dispositions sur lesquels Carpenter émet des doutes, pour croire

<sup>1</sup> "Quelques mots sur les relations du Système circulatoire chez les Echinides," 'Zool. Anzeiger,' viii Jahrg., 1885, p. 83.



ne m'être pas trompé." To this I can make no further reply than that the injection method should not be relied on too implicitly in the decision of a disputed point of minute anatomy. Apart from the divergent results of Perrier and Koehler respecting the anatomy of the vascular system in the Urchins, there is a long series of statements about that of the Star-fishes, which are principally based upon the results of injection, and are hopelessly at variance with one another.

Besides maintaining the truth of his previous descriptions, Koehler discusses some of the points wherein we differ. He expresses himself as utterly unable to find the pharyngeal blood-vessels which Teuscher described as uniting the oral blood-vascular ring (auct) with the radial vessels; and he says point-blank that these vessels do not exist,<sup>1</sup> although their presence appeared as theoretically probable to him as it has to me. For this reason I may have somewhat overrated the value of Teuscher's observations; but, on the other hand, Koehler seems to me to have depreciated them very considerably when he says:

"Il dit qu'ayant remarqué sur les coupes du pharynx cinq lacunes il a pensé que ces lacunes correspondaient à cinq vaisseaux, que ces cinq vaisseaux devaient probablement aller se jeter dans un anneau péri-buccal et qu'ils feraient ainsi communiquer cet anneau avec son vaisseau perinervien. Comment? il ne le dit pas. Carpenter parle de suppositions dans sa note; on peut juger par ce qui précède la valeur réelle des observations de Teuscher dont il défend les conclusions."

Teuscher's description<sup>2</sup> of a horizontal section of the pharynx (fig. 5) is as follows:

"Zwischen je zweien dieser Ligamente, auf der Mitte jeder Leiste, erscheint an jeder derselben eine Gefäßöffnung (*bg.*). Nach meiner ueberzeugung gehören diese Oeffnungen fünf Blutgefässen an, welche nur aus dem Blutgefässring entspringen können. Nach unten (fig. 6) sieht man diese Gefässe sich von der Wand des Pharynx entfernen, um über den an der Mundbasis liegenden Nervenring (*nr.*) (wovon unten) hinwegzutreten."

Now it does not appear to me likely that Teuscher can have

<sup>1</sup> 'Zool. Anzeiger,' 1885, p. 80.

<sup>2</sup> "Beiträge zur Anatomie der Echinodermen," iv, 'Jenaische Zeitschrift,' Bd. x, pp. 520, 521, Taf. xx, figs. 5, 6.

inserted these vessels in the figures of his vertical and transverse sections of the pharynx, without having seen something which he might have mistaken for vessels. But, according to Koehler, nothing of this kind is present; nor will anyone ever discover such vessels, even with the eye of faith. "Les deux vaisseaux radiaux ne communiquent qu'avec l'un des deux anneaux," that, namely, which communicates with the exterior through the water-tube and madreporite, and is generally known as the water-vascular ring.

Unfortunately, however, Koehler's statements upon this point have not been supported by any figures; and in reply to my remark to this effect Koehler says: "En ce qui concerne les figures, je crois en avoir donné d'assez nombreuses et d'assez démonstratives, mais à propos de la circulation de l'oursin il m'a semblé inutile de représenter à nouveau des dispositions déjà figurées par Perrier." But since the second radial vessel (the blood-vessel, as I regard it) was entirely unknown to Perrier, Koehler would have done well to give a figure showing its (supposed) junction with the radial water-vessel which was described and figured by Perrier.<sup>1</sup> Such a figure would go far to support Koehler's assertion, which, if true, must necessitate a considerable change in the generally received ideas respecting the morphology of the Echinoderm vascular system. I presume that it would not be difficult to obtain a series of sections through the part where the double radial vessels "become simple." But the figure illustrating this point, whether of an injected preparation or of a section, has yet to be drawn; and we must content ourselves for the present with Koehler's bare statement of the fact.

He is surprised at my representing him as considering the "madreporic canal" which runs from the organ of excretion of *Spatangus* towards the madreporite as the water-tube. I must apologise if I have misunderstood him; but I used the word water-tube=Steincanal=canal du sable, as denoting the vessel by which the oral vascular ring that supplies the

<sup>1</sup> "Recherches sur l'appareil circulatoire des Oursins," 'Arch. de Zool., Exp. et gén.,' t. iv, 1875, p. 621, pl. xxiv.

ambulacral vessels communicates with the exterior. I believe this to be the generally accepted meaning of these three equivalent terms.

Now Koehler's injections passed out from the madreporic canal to the exterior; while he describes its inner end as in perfect structural continuity with the organ of excretion.<sup>1</sup> He speaks of "le canal du sable, qui présente chez les *Spatangues* une structure glandulaire sur une partie de son trajet;"<sup>2</sup> and the tubular communication of the organ of excretion with the oral ring in which the radial (blood-) vessels originate is continually referred to by him<sup>3</sup> as the "canal du sable." Thus, then, the madreporic canal and its continuation through the organ of excretion towards the oral vascular ring form the only communication between the latter and the exterior, according to Koehler's views. He himself calls one part of this line of communication by the French equivalent for "water-tube;" and I cannot see, therefore, why he is surprised at my supposing him to take the same view of that other part of it which lies immediately beneath the madreporite, and is described by himself as opening to the exterior through its pores. In what other way can the following sentence be explained? "*J'étudierai plus loin les relations du canal du sable avec cet organe (of excretion) et sa termination vers la plaque madreporique.*"<sup>4</sup>

It is just possible that as Koehler does not believe in the general independence of the water-vascular and blood-vascular systems, the expression "water-tube or stone-canal" has not the definite meaning for him which is attributed to it by those who regard the stone-canal as a part of the water-vascular

<sup>1</sup> 'Recherches,' pp. 98, 99.

<sup>2</sup> *Ibid.*, p. 110.

<sup>3</sup> *Ibid.*, p. 98. "C, canal du sable," on pl. i, figs. 1—3; pl. ii, figs. 6, 8, 10, 11; pl. iii, figs. 14, 15.

<sup>4</sup> *Op. cit.*, p. 91. The italics are mine. If Koehler does not consider his "madreporic canal" as the water-tube or stone-canal, he would have done well not to call it by this name, which has been used by many writers instead of stone-canal (Huxley's 'Invertebrata,' pp. 558, 576).

system only, and would not give this name to any vessel connected with either end of the ovoid gland.

I do not regret my remark, however, as it has drawn from him a definite statement of his views; and if I interpret them aright, I am glad to find them more in accordance with those which I expressed in my previous note than I had any reason to expect. He says:

“Je considère le canal du sable,<sup>1</sup> la glande et le canal madréporique chez le *Spatangue* comme respectivement homologues au canal glandulaire, à la glande ovoide et son conduit excréteur chez l'*Oursin*, et que le canal du sable de ce dernier est représenté chez le *spatangue* par le canal onduleux qui accompagne l'oesophage<sup>2</sup> plus le canal à épithélium cylindrique dont il était question tout à l'heure. Ces deux canaux ne représentent que les deux extrémités du canal du sable dont la région moyenne aurait disparu et dont l'extrémité apicale aurait perdu les relations qu'elle a chez l'*Oursin* avec la plaque madréporique.”

With the exception of the second half of the last sentence this is precisely the position which I took up in my previous note<sup>3</sup>. Our only point of difference appears to be the following one. The canal with columnar epithelium is described by Koehler, on the results of injection<sup>4</sup> as losing itself “dans les lacunes du tissu conjonctif.” Teuscher<sup>5</sup> spoke of it as “Der Steincanal, welcher an seinem Cylinderepithel leicht kenntlich ist;” and he supposed it, though erroneously so, as Koehler has shown, to be continuous with the tube which unites the organ of excretion with the oral blood vascular-ring, *i. e.* Koehler's “canal du sable.” Teuscher evidently assumed, though he nowhere demonstrated, that it opened to the exterior through the madreporite; but this connection is denied by Koehler,<sup>6</sup> though he does not support his statements by figuring any sections which show the gradual subdivision of this canal, as described by him.

Like myself, however, he considers it as homologous with the dorsal end of the water-tube (canal du sable) of *Echinus*;

<sup>1</sup> This is coloured blue and lettered C, on pls. i—iii of Koehler's memoir.

<sup>2</sup> C' of Koehler's figures.

<sup>3</sup> This Journal, vol. xxiii, pp. 607—609.

<sup>4</sup> ‘Zool. Anzeiger,’ 1885, p. 82.

<sup>5</sup> *Loc. cit.*, p. 532.

<sup>6</sup> ‘Recherches,’ p. 99.



while we both regard the ventral end of this water-tube as represented in *Spatangus* by the incomplete sinuous canal (C' of Koehler's figures) which lies along the gullet and starts from the water-vascular ring (auctorium).

Koehler attributes no special functional importance to this discontinuous water-tube; whereas I have suggested that its two ends may correspond respectively to the water-pores on the disc of a Crinoid and the water-tubes by which the water-vascular ring communicates with the body cavity. There would be a difficulty about this, however, if Koehler is right in saying that the tube with columnar epithelium, Teuscher's Steincanal, "ne débouche pas au dehors et ne tarde pas à se perdre au milieu des interstices du tissu conjonctif."<sup>1</sup>

At the beginning of Koehler's statement of his views which I have just quoted, he uses the term "canal du sable" for an organ in *Spatangus* which he and I both believe to be homologous, not with the similarly named vessel in *Echinus*, but with the "glandular canal" that unites the ovoid gland with the oral blood-vascular ring of this type. I rather wonder, therefore, at his giving the same name to two vessels which he does not consider as homologous. According to his views they have the same function, viz. that of effecting the communication between the conjoint vascular system and the exterior, the work of the glandular canal and water-tube in *Echinus* being performed in *Spatangus* by the former alone, owing to the incomplete development of that part of the system which is homologous with the water-tube of *Echinus*. But would it not have been more rational to call the "canal du sable" of *Spatangus* by the name of that organ, the glandular canal, to which it is unquestionably both homologous and analogous in *Echinus*? As it is, however, Koehler has preferred to use the name "canal du sable" for this tube; and most readers would therefore regard him as attributing to it the function of admitting water into the vascular system. This, be it remembered, must take place through the organ of excretion, if Koehler's views are the true ones. But, if he will pardon me for saying

<sup>1</sup> 'Recherches,' p. 99.

so, there is still a certain amount of doubt respecting the communication of this organ with the exterior. Even if this be admitted, however, the fact still remains that the "canal du sable" of *Echinus*, and the tube to which Koehler gives the same name in *Spatangus*, do not communicate with the same vascular ring. The former joins the water-vascular ring (auct) which communicates with the tentacular system; while the latter is connected, not with the water-vascular ring of *Spatangus*, but with the blood-vascular ring; so that even if the community of the two vascular systems be admitted, the "canal du sable" of the two genera are not homologous, and it therefore seems to me very undesirable that they should both receive the name which is strictly applicable to one of them only.

Partly in consequence of this want of precision in his nomenclature, and partly by the omission of half a dozen words in one of my sentences, Koehler has been led to comment on what he believes to be an inconsistency between two passages which he quotes from my previous paper. In the first one,<sup>1</sup> I expressed the belief that the canal which joins the excretory organ in *Spatangus* with the oral ring, and is called by Koehler the "canal du sable," does not really belong to the water-vascular system, but corresponds to the "glandular canal" of *Echinus*. Koehler<sup>2</sup> remarks that he had already pointed out this latter homology, as indeed I had stated in my earlier note.<sup>3</sup> But then he goes on to say, "Puis à la page suivante Carpenter ajoute. 'Koehler regards the stone canal of *Spatangus* as homologous with the glandular canal of *Echinus*,'" and he endeavours to find in my subsequent remarks an expression of a theory inconsistent with his belief and my own.

What I really wrote was—"Koehler regards the organ which is commonly called the stone canal of *Spatangus*, as homologous with the glandular canal of *Echinus*, on

<sup>1</sup> This Journal, vol. xxiii, p. 607.

<sup>2</sup> 'Zool. Anzeiger,' 1885, p. 81.

<sup>3</sup> This Journal, vol. xxiii, p. 609.

account of its relation to the excretory gland. It appears to me, however, that Teuscher's identification of the canal with columnar epithelium, found by him at the apical pole, as the water-tube, is more correct than Koehler's view of what is evidently the same structure."

The words in italics were omitted by Koehler in his quotation, and he thus entirely altered the meaning of my sentence. I never referred directly to "the stone canal" of *Spatangus*, as would appear from Koehler's quotation; and had I done so, I should never have given this name to a tube which communicates, not with the water-vascular ring (auctorum), but with the excretory gland at one end, and with the oral blood-vascular ring at the other. Not wishing to be dogmatic, I avoided giving a definite name, as Koehler has done, to either of the canals between the oral rings and the madreporite. Koehler, however, first attributes to me an expression which I purposely refrained from using (*i. e.* in propria persona), and then interprets it according to his own ideas, which I am far from sharing.

In writing of "the organ which is commonly called the stone-canal of *Spatangus*," I was merely referring to the homologue of the glandular canal of *Echinus*. Teuscher<sup>1</sup> calls it the "Steincanal," and noted the presence of a second vessel by its side where it lies along the gullet. Hoffmann<sup>2</sup> gave this name to the two vessels together, not having been able to differentiate them; while Koehler<sup>3</sup> speaks of the "canal du sable" as double along the whole length of the gullet, but as single for the rest of its course until it joins the organ of excretion, just like the glandular canal of *Echinus*, with which both he and I believe it to be homologous.

I was perfectly right, therefore, in referring to it as the stone-canal of authors. But as all agree in describing its connection with the ovoid gland, and I do not believe that this organ

<sup>1</sup> Loc. cit., p. 534.

<sup>2</sup> "Zur Anatomie der Echinien und Spatangien," 'Niederl. Archiv f. Zool.,' Bd. i, 1871, pp. 85, 86.

<sup>3</sup> 'Recherches,' p. 92.

communicates with the exterior, I certainly never spoke of it as the stone-canal, as quoted by Koehler. On the other hand, I believe that Teuscher was right in giving this name to the canal with columnar epithelium at the apical pole. Koehler agrees with both Teuscher and myself in considering it as homologous with the dorsal end of the "canal du sable" in an *Echinus*. But he nevertheless prefers to give this name to the homologue in *Spatangus* of a totally different structure, viz. the glandular canal of *Echinus*. This appears to me to be very undesirable. The expressions stone (or sand) canal, water-tube, Steincanal, canal du sable, &c., have hitherto been understood as referring to the tube which joins the primary "dorsal pore" of an Echinoderm larva with the developing water-vascular ring and its tentacular apparatus. This remains as a continuous tube in *Echinus*, alongside the ovoid gland and its connections at both ends. In *Spatangus*, however, only the extremities of this primary tube are left, the middle portion having disappeared. Koehler admits this;<sup>1</sup> but nevertheless he transfers the name "canal du sable" to another structure altogether, which, on his own showing, is in no communication whatever with the water-vascular ring and tentacular apparatus; and for the undoubted homologue of which in *Echinus* he would not think of using the name canal du sable.

We have already seen that Perrier's statements respecting the relation of the ovoid gland of *Echinus* with the exterior have been repeated by Koehler, who now speaks of them as "relations qu'on ne peut nier puisqu'on voit dans les injections, la matière se répandre au dehors à travers les pores de la plaque madréporique."<sup>2</sup> I hope that I shall not be considered discourteous if I still avow myself a sceptic upon this point; and I will try to explain my reasons for my doubts. They are of two kinds, partly theoretical and partly practical.

In the present state of morphological teaching it is the general practice to put before the student a series of typical

<sup>1</sup> 'Zool. Anzeiger,' 1885, p. 82.

<sup>2</sup> 'Zool. Anzeiger,' 1885, p. 81.



animals, with whose morphology he may make himself thoroughly acquainted. This method depends upon the very general assumption that the other members of the group of animals to which each type form belongs will resemble it in all those essential characters by which it differs from the other types. Next to the radial symmetry and the peculiarities of the skeleton, there is, I take it, no feature which is so eminently characteristic of Echinoderms as the presence of two sets of radial vessels, the water-vessels and the blood-vessels of authors; and of two corresponding vascular rings, the one communicating with the exterior through the stone-canal, and the other connected with the cavities of the remarkable glandular organ which was formerly considered as a heart.

Now the most careful observations which have yet been made upon the Starfish (the typical Echinoderm of every teacher) go to show, not only that the so-called water-vascular and blood-vascular systems are fundamentally independent of one another, but also that the latter does not communicate with the exterior through the madreporite, as the former does; and I have a strong conviction that equally careful observations, conducted by the same rigorous methods, will show that these characters exist in the Urchins. They have been described as presenting themselves in Ophiurids and in Crinoids. But although the accuracy of these descriptions has been called in question by the French zoologists, no proof has yet been furnished that they are incorrect. Thus, for example, Ludwig describes the single water-pore of Ophiurids as leading (directly or indirectly) into the stone-canal; while the so-called heart "endigt über der Innenseite der Madreporenplatte neben der Stelle, an welcher sich der Steinkanal mit der Madreporenplatte verbindet."<sup>1</sup> He figures some selected horizontal sections through the madreporite, which, as usual, fully bear out his statements.

Then comes Apostolidès<sup>2</sup> who tells us how "Chez les

<sup>1</sup> "Neue Beiträge zur Anatomie der Ophiuren," 'Zeitschr. f. wiss. Zool., Bd. xxxiv, 1880, p. 351. Taf. xiv, figs. 1—3.

<sup>2</sup> "Anatomie et Développement des Ophiures," 'Arch. de Zool. exp. et Gén.,' vol. x, 1881, p. 25 (of separate copy).

*Ophiocoma* le canal aquifère vient aboutir directement à l'extérieur, par un pore unique sans canal. Le canal du pore suit directement le canal aquifère, dont il n'est qu'un prolongement qui se rencontre chez les individus adultes. Chez les *Ophiothrix*, les choses ont lieu comme chez l'*Ophiocoma nigra*." But then he goes on to tell us how in *Ophiothrix rosula* it is easy to expose the heart or piriform gland by slitting up the envelope which surrounds it and the stone-canal; and it is then "impossible de ne pas voir la communication directe de la glande piriforme avec l'extérieur." Farther on again he says, "Son conduit est extrêmement apparent, et ainsi aucune erreur ne peut exister sur ce point."

But if the single pore-canal of the madreporite is the direct continuation of the stone-canal, how can the duct of the piriform gland open externally? Apostolidès is silent upon this point; and his figures<sup>1</sup> (like that given by Perrier of the corresponding parts in an Urchin<sup>2</sup>) merely show the termination of both "duct" and stone-canal on the inner side of the madreporite. There is no indication whatever that the former opens externally through the pore, although Apostolidès' injections have caused him to have no doubt whatever concerning the existence of this communication. He tells us that he has confirmed the results of his injections by the section method. But he does not figure a single section showing how the duct of the piriform gland opens externally; and I much doubt whether he or any one else will ever do so.

I feel therefore that we are fairly entitled to use our present knowledge of the vascular system in the Brachiate Echinoderms as a basis for criticising the descriptions of its peculiarities in the Urchins which have been published by Perrier and Koehler. The researches of these authors have been principally carried on by means of injections, and not by the section-method which has been chiefly employed in the investigation of the Brachiate Echinoderms. Each plan has its advantages; but it will be generally admitted that the

<sup>1</sup> 'Arch. de Zool. exp. et Gén.,' vol. x, pl. viii, fig. 6, and Pl. ix, fig. 8.

<sup>2</sup> Ibid., vol. iv, pl. xxiii, fig. 1.

former is less satisfactory, when used singly, than the latter; and that its results require to be checked by a careful anatomical investigation before they can be trusted too implicitly.

I am well aware of the danger of placing too much reliance upon a theoretical morphology of Echinoderms: and I have so often alluded to it in discussing the nervous system of Crinoids<sup>1</sup> that I am not surprised to be told that my doubts as to the accuracy of the French observations respecting the communication of the ovoid gland of an Urchin (or Ophiurid) with the exterior are due to the influence of preconceived theoretical ideas. But, all the same, I find it difficult to believe that there should be such a difference between the vascular systems of Urchins and Starfishes respectively as is revealed by a comparison of the results of Perrier and Koehler on the one hand, and of Ludwig on the other.

The statements of the French authors are based upon the results of injections. So were the assertions of Hoffmann, Greeff, and Teuscher respecting the communication of some of the pores in the madreporite of a Starfish with the tubular space which surrounds both the ovoid gland and the stone-canal. Ludwig, however, working with four different species, made sections of the madreporite in three different planes, and dissected out its surroundings under a lens: "In allen Fällen war das Resultat dasselbe. Nicht eines der Porencanälchen führt wo anders hin als in den Steincanal (oder dessen nachher zu besprechende ampullenförmige Erweiterung); das gesammte Canalsystem der Madreporenplatte steht einzig und allein in Zusammenhang mit dem Steincanal, aber nicht mit dem schlauchförmigen Canal, noch auch mit irgend einem anderen Hohlraum."<sup>2</sup>

This very definite statement has never been contradicted, even by Messrs. Perrier and Poirier, who while asserting

<sup>1</sup> The present position of this question has been described by a distinguished biologist as "the triumph of physiology over morphology."

<sup>2</sup> "Beiträge zur Anatomie der Asteriden," 'Zeitschr. f. wiss. Zool.,' Bd. xxx, 1878, p. 104.

the glandular nature of the so-called heart of a Starfish,<sup>1</sup> say not a word respecting its communication with the exterior through the madreporite, although Perrier had previously described this communication in the Urchins. This omission is a significant one. Then, again, Jourdain,<sup>2</sup> who seems to have been the first to describe the glandular appearance of the supposed heart, not only gave no account of its having any communication with the exterior through the madreporite, but positively asserted that the pore-canals of this plate have no internal connection otherwise than with the water-tube, just as described by Ludwig some years later.

The latter author devoted some attention to the dorsal termination of the ovoid gland of a Starfish, and he found that, after passing through the aboral vascular ring, it entered "die kleine Höhlung welche die Ampulle der Madreporenplatte enthält . . . Das Herzende durchsetzt diese Höhlung (fig. 9) und befestigt sich dann schliesslich in ihr und zwar in ihrem zumeist dem Centrum der Rückenhaut zugekehrten Theile (figs. 10, 11). Soweit meine Beobachtungen reichen, gehört derjenige Theil der Höhlenwandung, an welchem sich das Herz inserirt, nicht mehr der Madreporenplatte selbst an, sondern dem unmittelbar daran austossenden Bezirke der Körperwand."<sup>3</sup>

Let us compare with the above statements the description given by Perrier and confirmed by Kochler respecting the dorsal termination of the ovoid gland in an Urchin. Both authors rely principally on the injection method. Perrier tells us that "La matière colorante, après avoir rempli la cavité cardiaque, passe dans un canal qui fait suite à la pointe supérieure du cœur et va remplir un espace infundibuliforme compris entre la plaque madréporique et la membrane de revêtement

<sup>1</sup> "Sur l'Appareil circulatoire des Etoiles de mer," 'Comptes Rendus,' March 6th, 1882, t. xciv, pp. 658—660.

<sup>2</sup> "Recherches sur l'Appareil circulatoire de l'Etoile de mer commune (*Asteracanthion rubens*)," 'Comptes Rendus,' t. lxxv, 1867, pp. 1002—1004.

<sup>3</sup> Loc. cit., pp. 130, 131.



du test, qui, en ce point, n'est pas adhérente à la plaque madreporique." He then goes on to say that the pores of the madreporite open into this space, which "semble être tout d'abord une sorte de cloaque dans lequel viennent s'ouvrir le canal du sable et le canal issu de la pointe supérieure de l'organe que l'on considère comme un cœur."<sup>1</sup>

Definite as these statements are, they appear to me to rest upon insufficient evidence, as did those of Hoffmann respecting the Starfishes. If the pores of the madreporite in an Urchin really do lead into a cavity which lies beneath it, and receives the ends both of the stone-canal and of the duct issuing from the ovoid gland, Perrier or Koehler could surely have obtained sections or other preparations<sup>2</sup> in proof of their assertions. They may have done so; but, as the fact is one of considerable importance, they would have done well to illustrate it by figures. Ludwig figures several sections through the madreporite of a Starfish, and they completely bear out his statements which I have quoted above. Had Messrs. Perrier and Koehler done the same, the solution of the problem of the Echinoderm vascular system would have been very materially advanced.

Ludwig's remarks<sup>3</sup> upon the possible fallacies of the injection method are very much to the point, and if the internal connections of the pore-canals in the madreporite can be demonstrated in a Starfish a similar demonstration is surely possible in the case of an Urchin. But we have not had it as yet; and in the absence of this much-to-be-desired proof of the statements of MM. Perrier and Koehler I prefer to believe that the relations of the ovoid gland to the madreporite are the same in the Urchin as they are in the Starfish, according to Ludwig, *i.e.*, that the ovoid gland does not communicate with the exterior.

I have therefore practical reasons, besides the purely theo-

<sup>1</sup> 'Arch. de Zool. Exp. et Gén.,' t. iv, p. 613.

<sup>2</sup> The dissection which is represented in fig. 1, of Perrier's memoir, only shows this infundibuliform space from the outside. A larger figure of its internal arrangements would be interesting.

<sup>3</sup> Loc. cit., p. 103.

retical ones on which Koehler comments, for doubting his description of the communication of the two vascular systems of an Urchin, both with one another and with the exterior. But at the same time I am fully prepared to abandon my doubts and to admit the truth of his views, when he can demonstrate the following propositions by the same methods as Ludwig employed in his work on the Starfishes.

1. The communication of the so-called excretory canal of the ovoid gland in an Urchin with the space beneath the madreporite, into which the pore-canals and the water-tube both open.

2. The connection of both the radial vessels of an Echinus with one oral ring (water-vascular, auctorum).

3. The connection of the intestinal vessel of *Spatangus* with both the oral rings.

In these days of an intensely elaborated technique and self-acting microtomes, it must surely be possible to obtain such a series of sections as would put the truth of Koehler's views beyond the reach of doubt; but if obtained they have not yet been figured. We are indebted to him for the rediscovery of the "glandular canal" of Echinus, by which the ovoid gland communicates with an oral blood-vascular ring. This connection was positively denied by Perrier,<sup>1</sup> as the result of unsuccessful injections. Koehler's injections were more fortunate, however, and he confirmed his results by making transverse sections of the combined water-tube and glandular canal,<sup>2</sup> which place his discovery upon a sure foundation. Can he not do the same for the three anatomical points mentioned above?

I trust that what I have written above will not be considered as wanting in courtesy to Mons. Koehler. We owe him such a heavy debt of gratitude for the advance which he has made in our knowledge of the Echinoid vascular system, that it seems almost ungracious to ask for further information. His descriptions of the radial blood-vessels, and of the glandular canal

<sup>1</sup> 'Arch. de Zool. Exp. et Gén.,' t. iv, p. 613.

<sup>2</sup> 'Recherches,' pl. vi, fig. 40.

between the ovoid gland and the oral blood-vascular ring only suggest the possibility of an even closer resemblance between the vascular systems of Urchins and Starfishes than has hitherto been thought possible.

Will he not complete his work, and give a convincing demonstration of the truth of his own statements, so as to disprove the views of those morphologists, like myself, who believe in the fundamental distinctness of the two vascular systems throughout the Stellerids, Crinoids, and Urchins?

Postscript.—Two more notes upon Crinoid Anatomy have been published by Professor Perrier<sup>1</sup> since I last wrote upon the subject in the pages of this Journal.<sup>2</sup> The second one, which has only appeared quite recently, closes as follows:—  
“Chez les Comatules comme chez les Oursins, ce qu’on a appelé l’appareil vasculaire est en communication avec le système des canaux ambulacraires.”

As regards the Urchins, the nature of the evidence on which Professor Perrier relies has been explained above, while I have discussed his statements about the Crinoids in my report upon the “Challenger” Crinoids.<sup>3</sup> When his illustrated memoir upon the Anatomy of *Comatula* has appeared, I intend to go into the whole question again, and I will only say at present that I have seen no evidence of a communication between water-vascular and blood-vascular systems in any of the five genera of Crinoids which I have examined, while neither Greeff, Teuscher, nor Ludwig make any mention of it. At the same time I am bound to confess that I never thought of looking for it at all until its existence was asserted by Professor Perrier, and I shall await his demonstration of it with very great interest.

<sup>1</sup> “Anatomie des Échinodermes ; sur l’organisation des Comatules adultes,” ‘Comptes rendus,’ tom. xviii, No. 23, June 9th, 1884, pp. 1448—1450; and “Sur le développement de l’appareil vasculaire, et de l’appareil genital des Comatules,” *ibid.*, tom. c, 16th February, 1885.

<sup>2</sup> “Notes on Echinoderm Morphology,” No. 3, “On Some Points in the Anatomy of Larval *Comatula*,” ‘Quart. Journ. Micr. Sci.,’ vol. xxiv, 1884, pp. 319—327.

<sup>3</sup> ‘Zool. Chall. Exp.,’ part xxxii, pp. 106, 40—407.









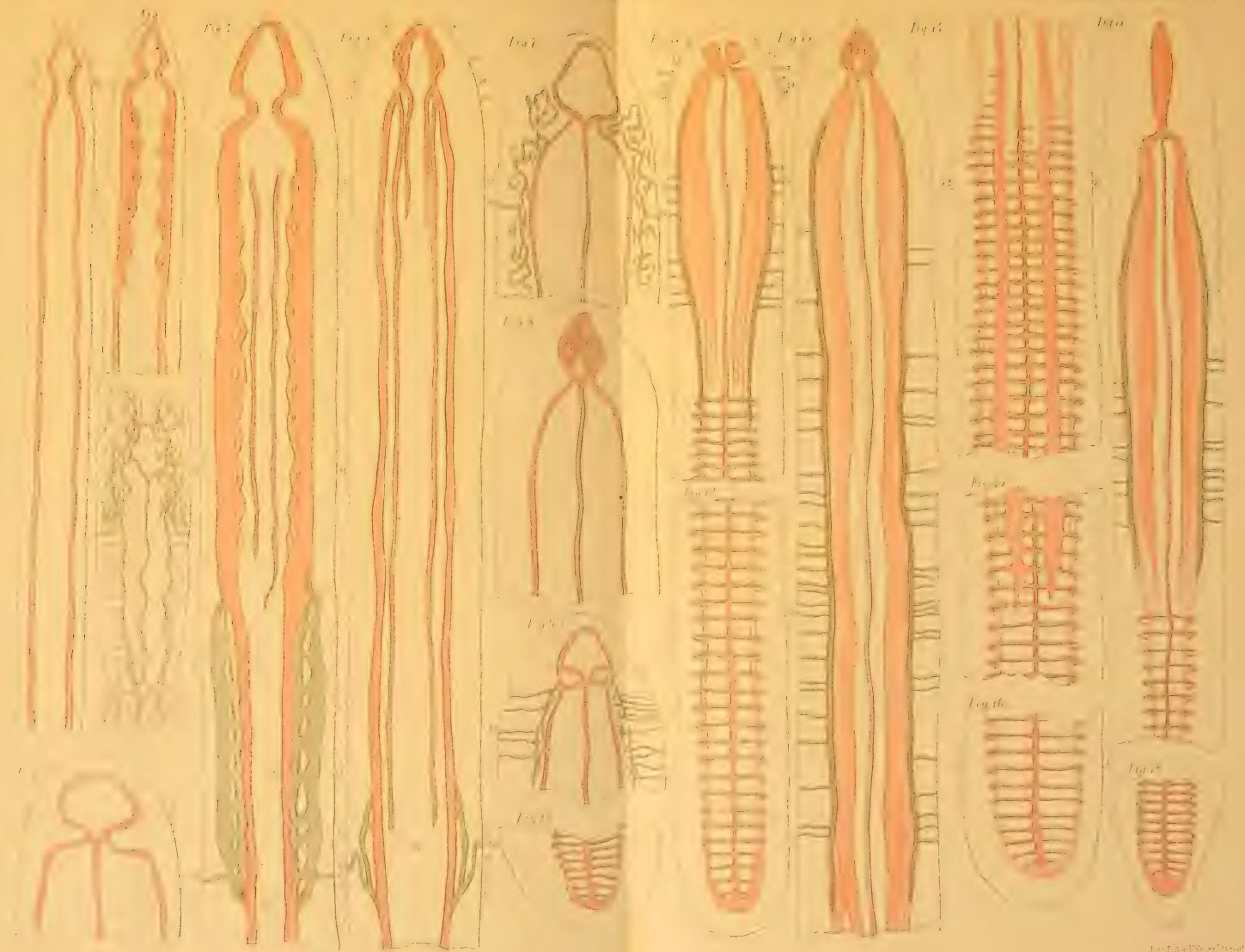






















Fig. 1.

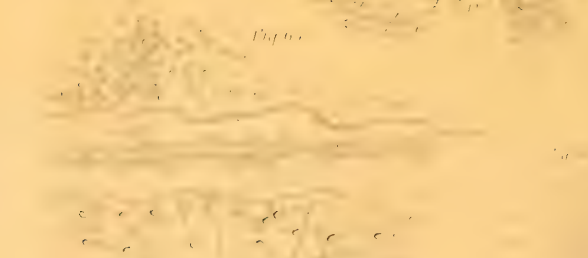


Fig. 3.

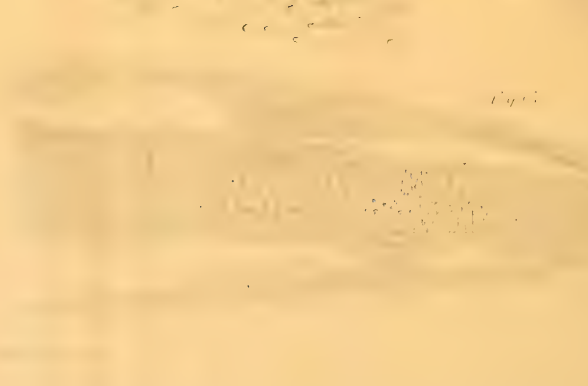


Fig. 5.



Fig. 6.

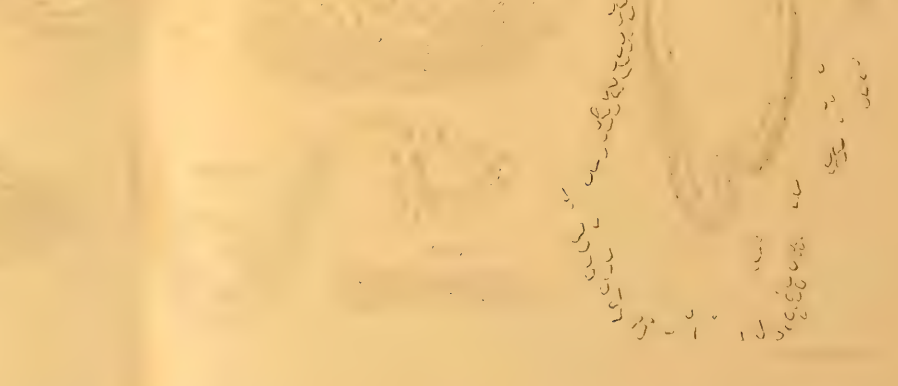


Fig. 7.

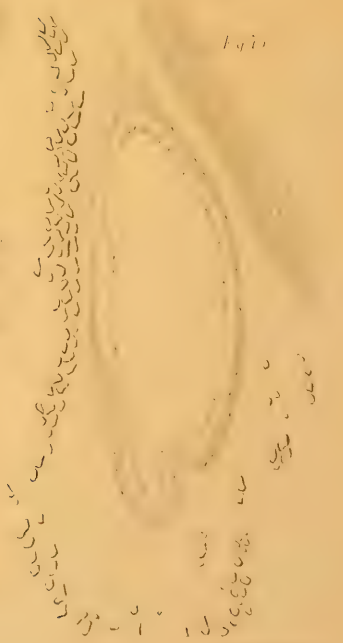


Fig. 8.



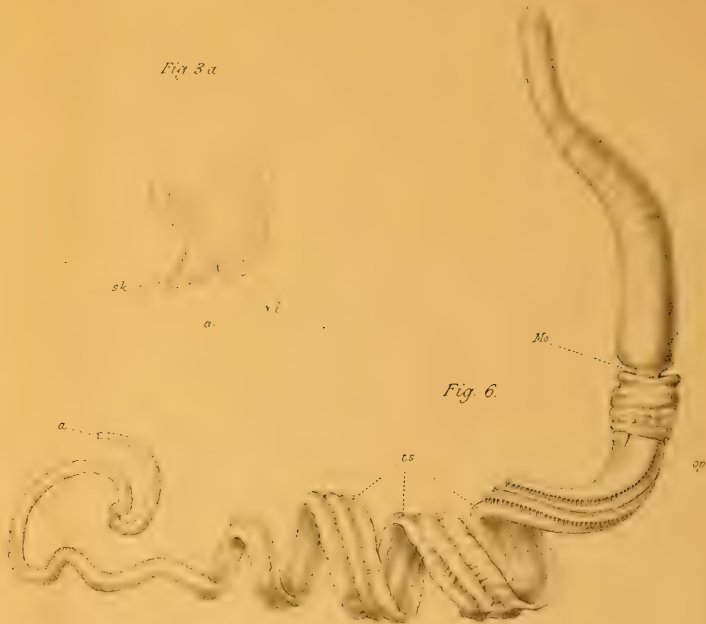




*Fig. 3a*



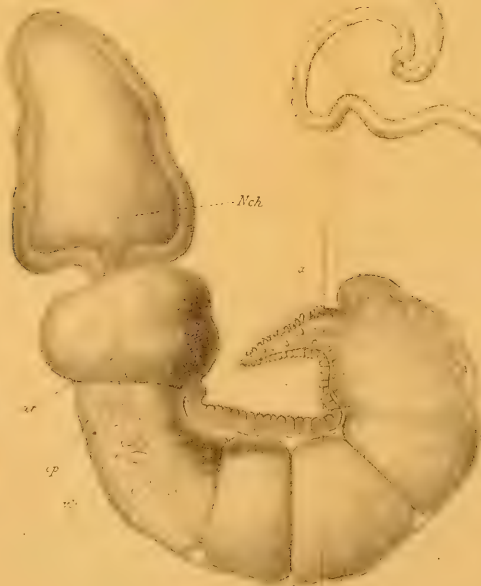
*Fig. 6*



*Fig. 3*



*Fig. 4*



*Fig. 5*

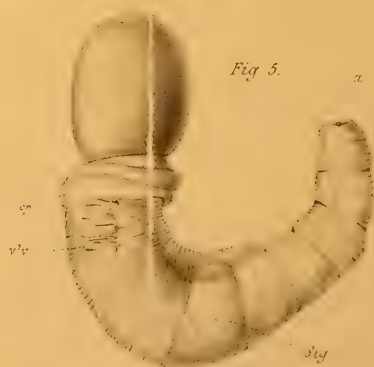










Fig. 7.



Fig. 8.

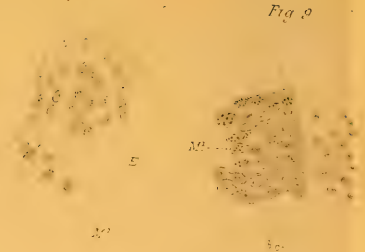


Fig. 9.



Fig. 10.



Fig. 11.

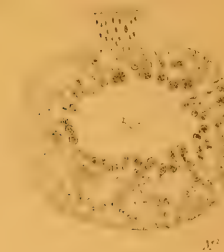


Fig. 14.

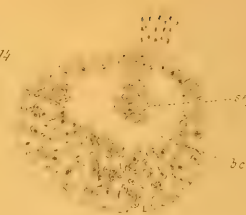


Fig. 13.

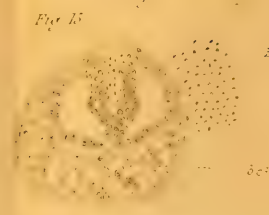


Fig. 12.

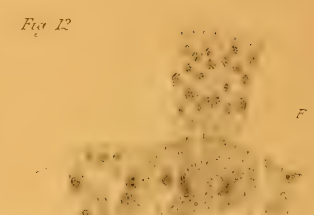


Fig. 15.

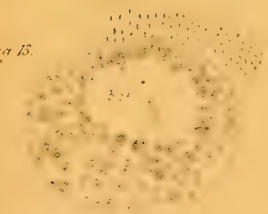


Fig. 17.

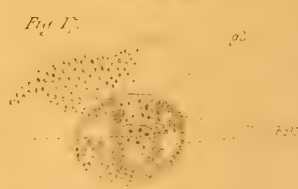


Fig. 18.



Fig. 21.



Fig. 19.



Fig. 20.



Fig. 16.

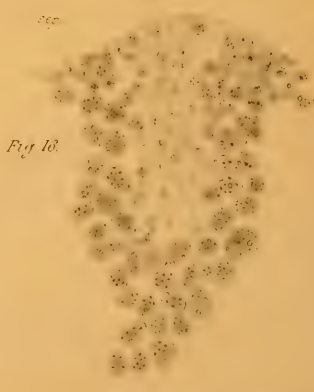












Fig. 22

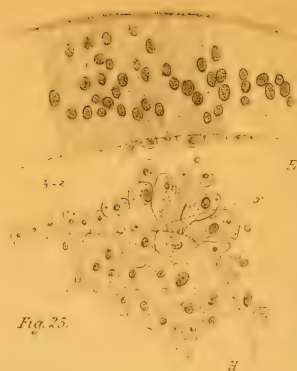


Fig. 25

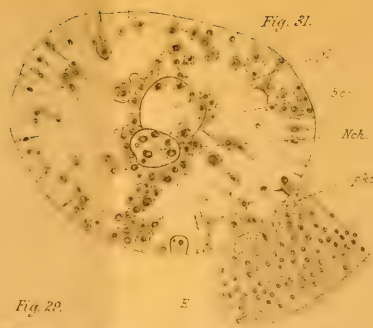


Fig. 29

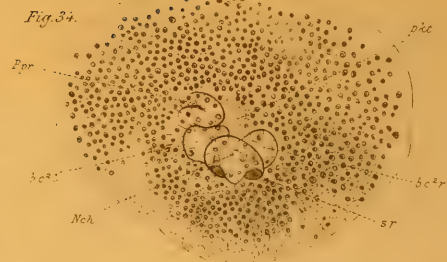


Fig. 34



Fig. 23



Fig. 26

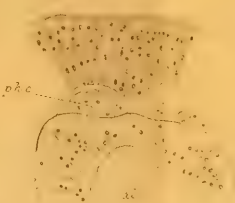


Fig. 35

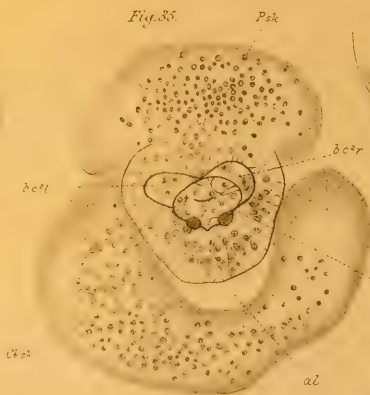


Fig. 32



Fig. 24

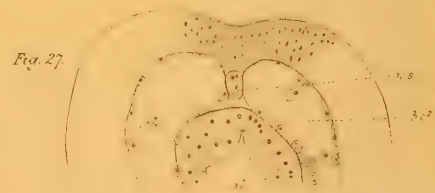


Fig. 27

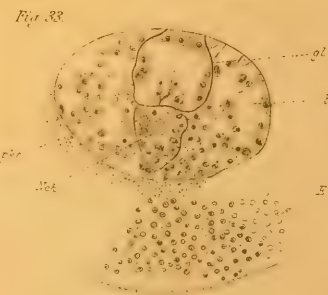


Fig. 33



Fig. 30



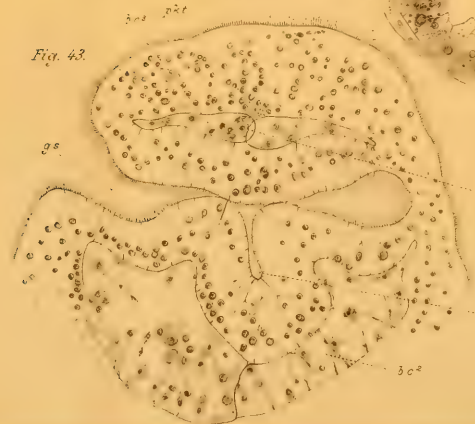
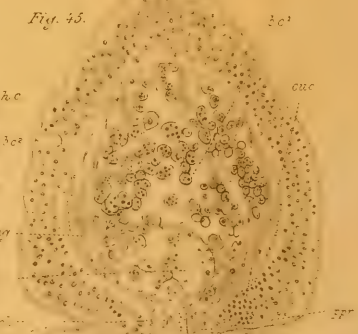
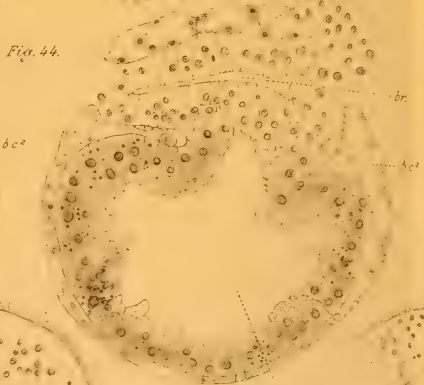
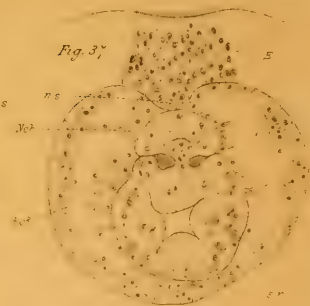
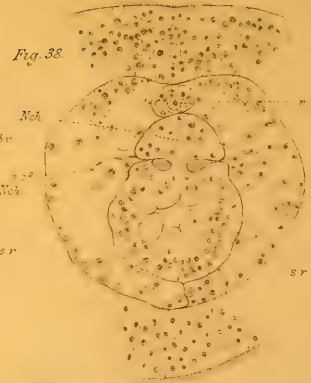
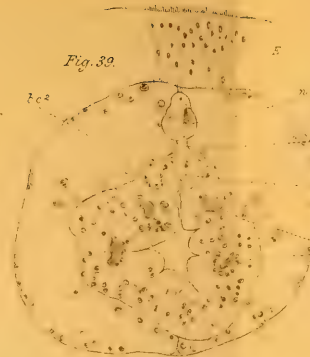
Fig. 28









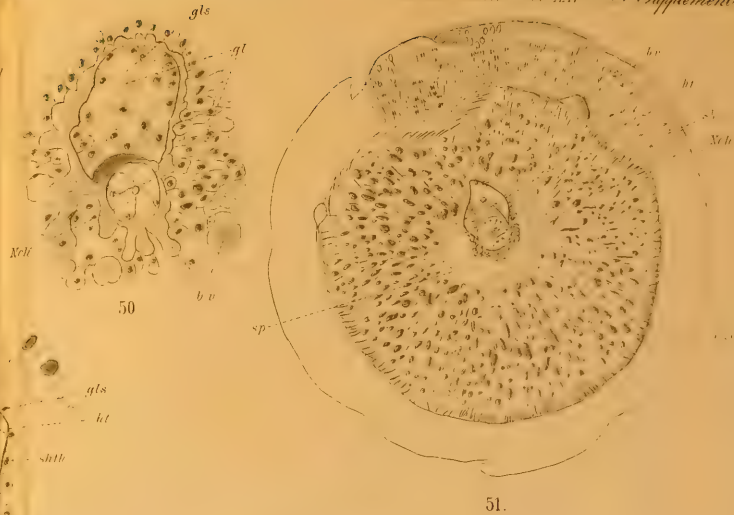
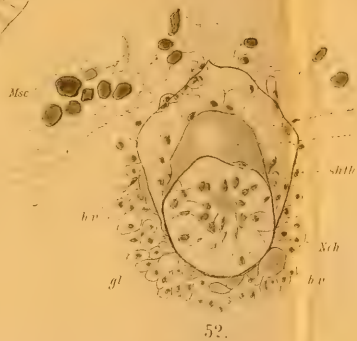
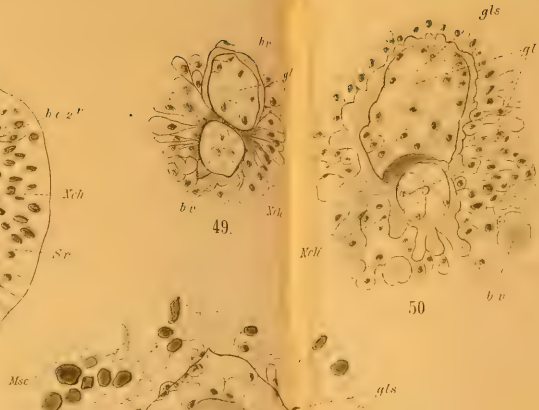
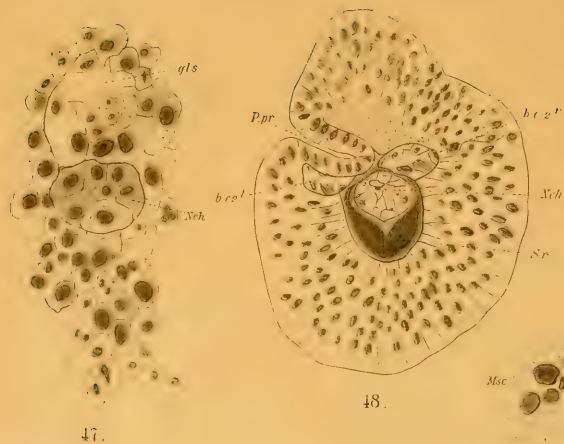






















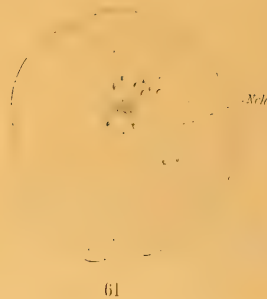
62



58.



63



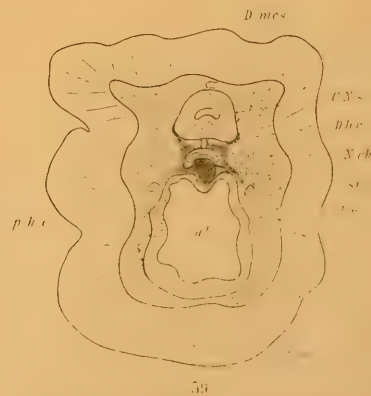
61



60.



57.



59









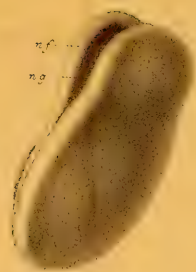


Fig. 1.



Fig. 2.

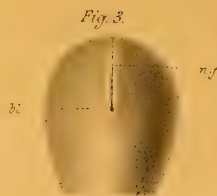


Fig. 3.

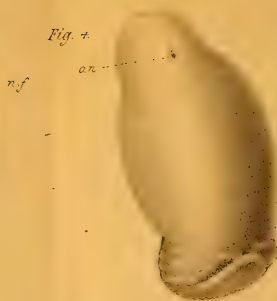


Fig. 4.



Fig. 5.

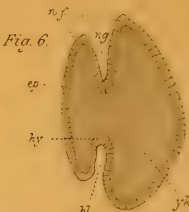


Fig. 6.



Fig. 7.



Fig. 8.

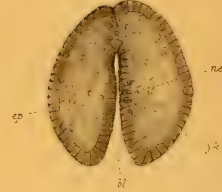


Fig. 9.



Fig. 10.



Fig. 11.

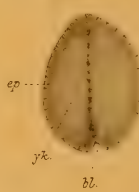


Fig. 12.



Fig. 13.

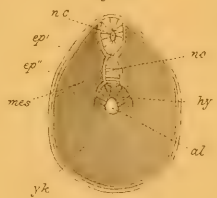


Fig. 14.



Fig. 15.

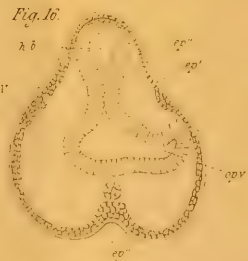


Fig. 16.

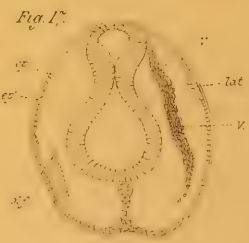


Fig. 17.

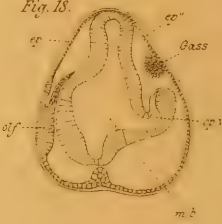


Fig. 18.



Fig. 19.



Fig. 20.

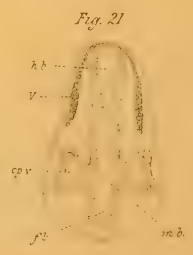


Fig. 21.

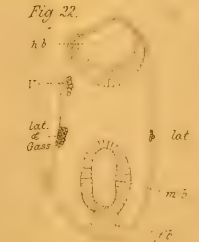


Fig. 22.

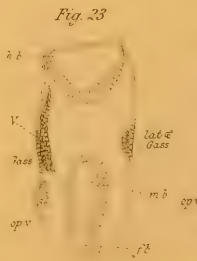


Fig. 23.

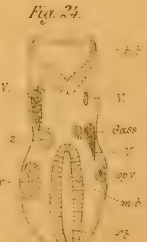


Fig. 24.

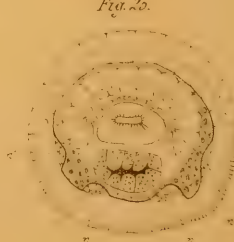


Fig. 25.















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